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Morphological and Phylogenetical Studies in the Isopoda (Crustacea). Part 2: The Pleopods and Uropods in the Phreatoicidea

By Friedhelm Erhard, Stuttgart

With 30 figures

Summary

The skeleton and musculature of the pleopods I–III and the uropods in the Australian species *Metaphreatoicus australis* (Chilton, 1891) (Phreatoicidea) are described. Each anatomical character, documented in *Metaphreatoicus,* is checked in further phreatoicidean species from Australia, Tasmania, India and South Africa to reconstruct groundpattern characters of the Phreatoicidea. The comparison with corresponding morphological data in the taxon Oniscidea indicates character transformations inside the Isopoda. First judgments on the polarity assessment of characters are discussed.

Zusammenfassung

Das Skelet und die Muskulatur der Pleopoden I–III und der Uropoden der australischen Art *Metaphreatoicus australis* (Chilton, 1891) (Phreatoicidea) werden dokumentiert. Jedes der an *Metaphreatoicus* beschriebenen anatomischen Merkmale wird an weiteren Phreatoicidea-Arten aus Australien, Tasmanien, Indien und Südafrika überprüft, um Grundplan-Merkmale der Phreatoicidea zu rekonstruieren. Der Vergleich mit entsprechenden morphologischen Daten des Taxon Oniscidea weist auf Merkmalstransformationen innerhalb der Isopoda hin. Erste Einschätzungen zur Lesrichtung der Merkmale werden diskutiert.

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1. Introduction

In the first part of the series "Morphological and Phylogenetical Studies in the Isopoda" (ERHARD 1998a) the necessity for detailed descriptions of anatomical characters was emphasized which might be useful to clarify existing inconsistancies in reconstructing the phylogenetic relationships between the main groups of the taxon Isopoda. The present study represents the second part of the description on the pleonal anatomy in the taxon Phreatoicidea. While the first part (ERHARD 1998a) deals with the skeleton and musculature of the pleon trunk in *Metaphreatoicus australis* (Chilton, 1891), the present publication treats the pleopods and uropods in the same species. The documented characters of *Metaphreatoicus* will be compared with the condition in other phreatoicidean species and with the situation in the Oniscidea (ERHARD, 1995, 1996, 1997, 1998b). The attempt is made to reconstruct groundpattern characters of the phreatoicidean and oniscidean pleopods and uropods.

Further parts of the publication series will follow. For the time being, the research program includes the documentation of the pleonal morphology in the Phreatoicidea, the description of the pleonal morphology in basal representatives of the Asel-

lota and a final analysis of the phylogenetic-systematic relationships between the three isopodan taxa Phreatoicidea, Asellota and Oniscidea.

2. Material, methods and abbreviations

2.1. Material

Phreatoicidea:

Metaphreatoicus australis (Chilton, 1891), Australia, New South Wales, Mt. Kosciusko (SMNS 14016, 14048)
Colubotelson joyneri searlei Nicholls, 1944, Australia, E-Victoria, Mt. Baw Baw (SMNS 14019)
Onchotelson brevicaudatus (Smith, 1909), Tasmania, Great Lake, southern bank (SMNS 14047)
Mesacanthotelson tasmaniae (Thomson, 1894), Tasmania, Great Lake, southern bank (SMNS 14047)
Paramphisopus palustris (Glauert, 1924), Australia, Western Australia, Lake Monger (SMNS 14119; ex AM P44487)
Phreatoicopsis terricola Spencer & Hall, 1896, Australia, Victoria, The Grampians (SMNS 14118; ex NMV J44869)
Nichollsia kashiensis Chopra & Tiwari, 1950, India, Banaras (SMNS 12149)
Mesamphisopus capensis Barnard, 1914, South Africa, Southern Cape, Zonder End Mountains (SMNS 15517; ex SAM A6052).

Oniscidea:

Ligia oceanica (Linnaeus, 1767), W-France, Brittany, Roscoff
Tylos ponticus Grebnitzky, 1874, Greece, island of Crete, E Sitia and island of Astipalea, Maltesana (SMNS 1242, 1549)
Mesoniscus alpicola (Heller, 1858), S-Germany, Bavaria, 6 km W Berchtesgaden
Titanethes albus Schiödte, 1849, Slovenia, 30 km S Ljubljana, Videm-Popeć, water cave (SMNS 5080, 5253)
Actaecia bipleura Lewis & Green, 1994, Tasmania, W Tamar River, W Greens Beach
Oniscus asellus Linnaeus, 1758, S-Germany, Baden-Württemberg, Tübingen.

2.2. Methods

Skeleton and musculature of the pleopods and uropods were reconstructed by manual micropreparation of fuchsine-stained material under the stereomicroscope and by the use of histological serial sections examined under the light microscope. The thickness of the histological sections was 7 µm, they were stained in haematoxylin-eosin and azan. The skeleton was also investigated after maceration in diethylenetriamine (KRAUTER 1980) and staining in chlorazol-black (CANNON 1937).

The morphological data on the isopodan pleopods and uropods are interpreted, if possible at all at the present state of knowledge, strictly according to the method of phylogenetic systematics proposed by HENNIG (1966).

2.3. Abbreviations

A	Point of articulation
AM	Australian Museum, Sydney, Australia
aPrAp	Anterior apophysis of pleopod protopodite
Chan	Anterior channel of appendix masculina
CLob	Medial coupling lobe of pleopod protopodite
cPtExt	Caudolateral extensions of pleotelson
dmUAp	Dorsomedial apophysis of uropod protopodite
En	Pleopod endopodite
EnDA II	Distal article of male pleopod endopodite II (= appendix masculina)
EnMb	Distal membranous part of pleopod endopodite
EnPA II	Proximal article of male pleopod endopodite II

EnScl Proximal sclerotized part of pleopod endopodite
Ep Lateral pleopod epipodite
Ex Pleopod exopodite
ExDA Distal article of pleopod exopodite
ExPA Proximal article of pleopod exopodite
ExPLob Proximal Lobe of pleopod exopodite
HSet Hooked or other coupling setae
Int Intestinum
IOEn Insertion opening of pleopod endopodite
M Muscle
Mb Membrane
mdApPt Mediodorsal apophysis of pleotelson tergite
Mm Muscles
NMV National Museum of Victoria, Australia
PlEm Pleon epimere
PlSt Pleon sternite
PlT Pleon tergite
Pp Pleopod
PpCh Pleopodal chamber
pPrAp Posterior apophysis of pleopod protopodite
Pr Pleopod protopodite
PrDA Distal article of pleopod protopodite
PrPA Proximal article of pleopod protopodite
Pt Pleotelson
PtAx Pleotelsonic apex
PtScl Ventrocranial pleotelsonic sclerite
PtSt Pleotelsonic sternite
PtT Pleotelsonic tergite
PtTr Pleotelsonic trunk
SAM South African Museum Cape Town, South Africa
Scl Sclerite
SMNS Staatliches Museum für Naturkunde Stuttgart, Germany
SpSet Spinose seta
StPr Sternal processus
Typh Ventral typhlosolis
UEn Uropod endopodite
UEx Uropod exopodite
UPr Uropod protopodite
vlUAp Ventrolateral apophysis of uropod protopodite
vPtExt Anterior lateroventral extensions of pleotelson.

3. Previous investigations and terminology

An overview on previous investigations on the pleonal skeleton and musculature in the Isopoda and other peracaridan taxa is given within the first part of the publication series at hand on isopod morphology and phylogenetics (Erhard 1998a: 5). Complementary, Wilson & Keable (in press) are presenting a computer-generated analysis on the systematics and phylogenetics of the Phreatoicidea.

The results of the investigation on the pleopodal skeleton and musculature of *Metaphreatoicus australis* will be compared here with literature data of comparative-anatomical studies on the main groups of the Oniscidea carried out by Erhard (1995, 1996, 1997, 1998b). Therefore, the consecutive numbering of the muscles refers to the nomenclature used in the above cited publications. Additional muscles, found in *Metaphreatoicus australis* or further aquatic isopods, not yet numbered in

the Oniscidea, are indicated by new numbers. Gaps in the numbering indicate muscles which are only present in subordinate oniscidean groups but not within the groundpattern of the Oniscidea or in the investigated phreatoicidean species.

For the purpose of consistency, the terms of skeletal structures, their abbreviations and their spellings were adopted from ERHARD (1995, 1996, 1997, 1998a, b).

4. Pleopods

The morphological study within the paper at hand treats mainly the skeleton and musculature of the pleopods I–III and the uropods in *Metaphreatoicus australis.*

After the description of one anatomical complex in *Metaphreatoicus,* characters are discussed by in- and outgroup comparisons and attempts are made to reconstruct groundpattern characters of the phreatoicidean and oniscidean pleopods and uropods.

The results were gathered chiefly from male specimens. It is emphasized if females were considered. Within the graphical reconstructions membranes are indicated by bold dotting.

4.1. Pleopods I

4.1.1. *Metaphreatoicus australis* (figs. 1–3)

4.1.1.1. Skeleton

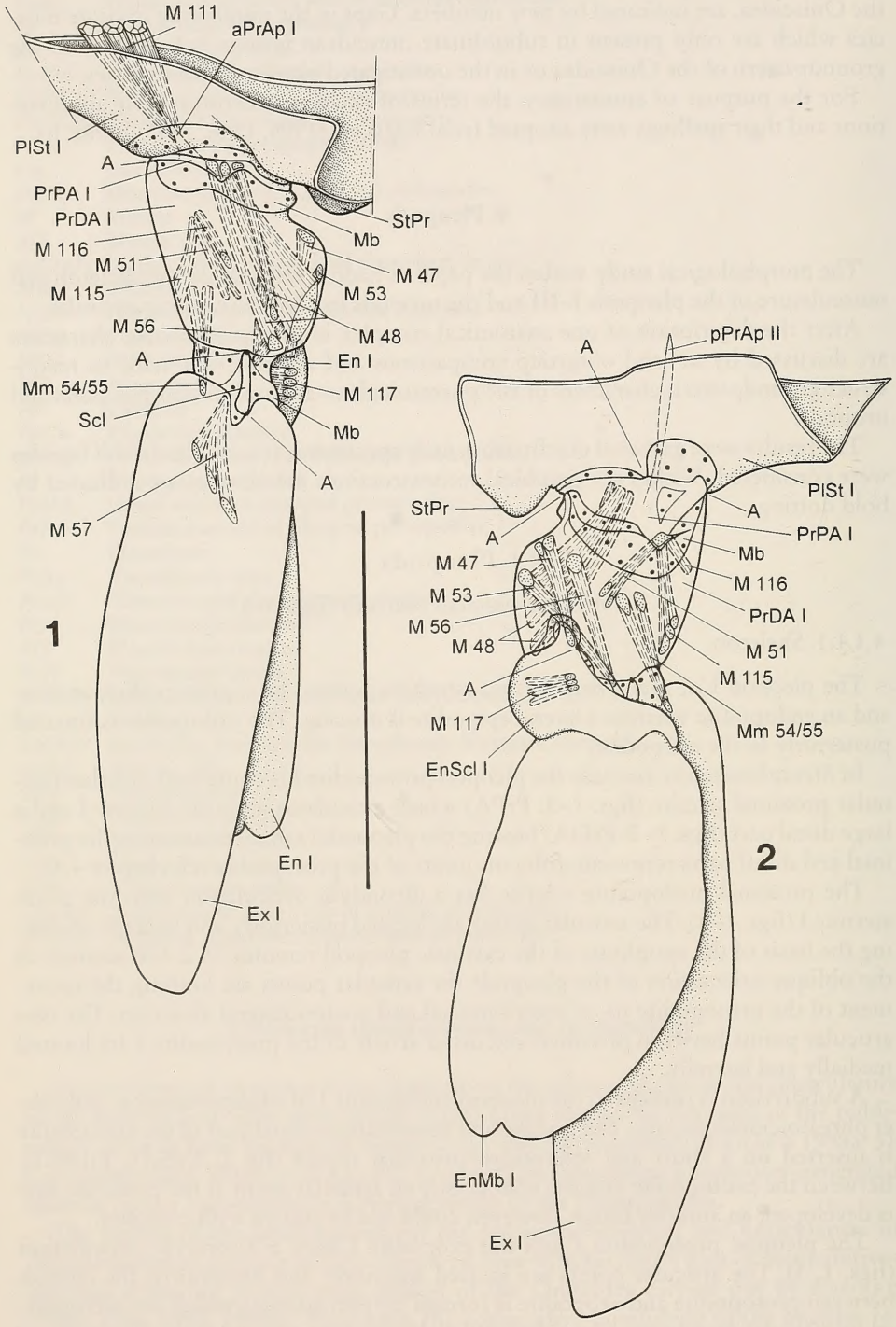
The pleopod I of *Metaphreatoicus australis* is formed by a protopodite, an exo- and an endopodite whereas a lateral epipodite is missing. The endopodite is situated posteriorly to the exopodite.

In *Metaphreatoicus australis* the pleopod protopodite I is composed of a short annular proximal sclerite (figs. 1–3: PrPA) which articulates with the sternite I and a large distal part (figs. 1–3: PrDA) bearing the pleopodal rami. Presumably, the proximal and distal parts represent different joints of the protopodite (cf. chapter 4.4).

The proximal protopodite sclerite has a dicondylic articulation with the pleon sternite I (figs. 1–3). The articular points are located posteriorly and laterally enclosing the basis of the apophysis of the extrinsic pleopod remotor M 2. On account of the oblique orientation of the pleopods the articular points are limiting the movement of the protopodite to an anteriomedial and posteriolateral direction. The two articular points between proximal and distal article of the protopodite I are located medially and laterally.

A subdivision is present in the pleopod endopodite I of *Metaphreatoicus* and other phreatoicidean species. The leaflike and membranous distal part of the endopodite is inserted on a short and sclerotized proximal region (fig. 2: EnScl I, EnMb I). Between the protopodite and the endopodite an articular point at the posterior side is developed; an anterior hinge, however, could not be shown with certainty.

The pleopod protopodite I and the exopodite I have a dicondylic articulation (figs. 1, 3). The articular points are located anteriorly and posteriorly, the contact between protopodite and exopodite is formed by two sclerites which are surrounded by articular membrane. Considering the oblique arrangement of the pleopods, an articulation axis is resulting which limits the movement of the pleopod exopodite I to a mediocaudal and laterocranial direction.



Figs. 1–2. *Metaphreatoicus australis*, ♂, right pleopod I. – 1. Anterior view; – 2. posterior view. – Scale: 1 mm.

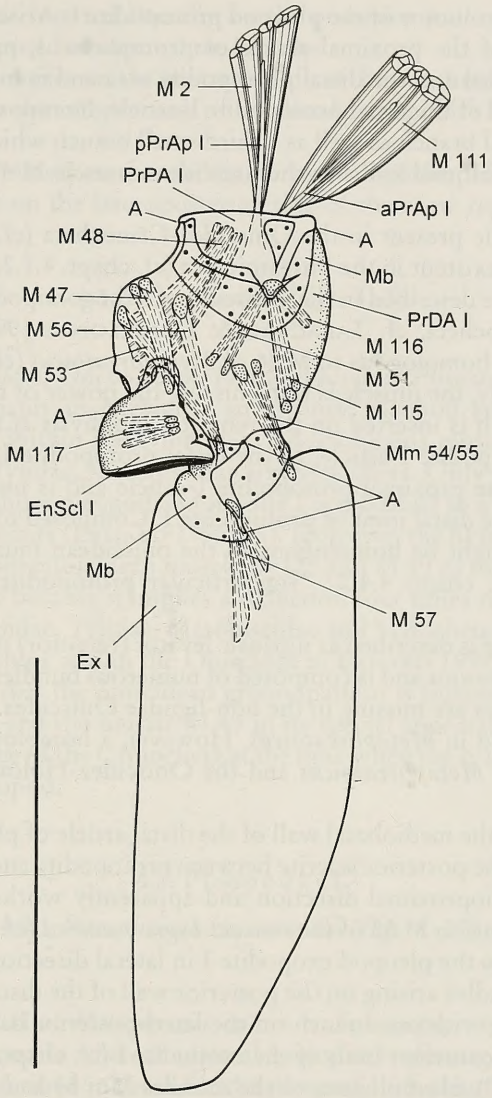


Fig. 3. *Metaphreatoicus australis*, ♂, right pleopod I in posterior view. Membranous distal part of the endopodite and pleon sternite I removed. – Scale: 1 mm.

The apophysis of the extrinsic promoter M 111 is located opposite to the apophysis of the remotor M 2, anteriolaterally on the proximal protopodite joint.

4.1.1.2. Musculature

M 47: Moves the endopodite I in medial direction. Arises on the mediobasal wall of the distal protopodite I-article and is inserted on the medioposterior basis of the endopodite I. Composed of two muscle bundles. Homologous to the oniscidean muscle M 47 and, probably, to M 52 of *Ligia oceanica* (cf. ERHARD 1995, 1996, 1997).

M 48: Intrinsic promotor of the pleopod protopodite I. Arises on an apophysis at the anterior wall of the proximal article of protopodite I, passes the membrane between the proximal and the distal protopodite area and is inserted mediodistally on the anterior wall of the distal protopodite I-article. Composed of a strong medial and a small lateral branch as well as a third small branch which runs anteriorly to the strong bundle. Homologous to the oniscidean muscle M 48 (cf. ERHARD 1995, 1996, 1997).

M 49: The muscle present in the Oniscidea-Crinocheta (cf. ERHARD 1995: 36), presumably, is not existent in the Phreatoicidea (cf. chapt. 4.1.2.: "M 117").

M 50: The muscle described in the Oniscidea-Orthogonopoda (= Mesoniscidae + Synocheta + Crinocheta, cf. TABACARU & DANIELOPOL 1996, ERHARD 1998b), probably, might be homologous to M 56 of *Metaphreatoicus* (cf. "M 56").

M 51: Presumably, the muscle is transmissing the power of the extrinsic pleopod remotor M 2, which is inserted on the remotor apophysis at the posterior side of the proximal protopodite I-article, to the distal protopodite I-joint. Arises on the posterior side of the proximal protopodite I-article and is inserted on the lateroposterior wall of the distal joint of protopodite I. Composed of two bundles. Probably, the muscle might be homologous to the oniscidean muscle M 51 present in *Oniscus asellus* (cf. chapt. 4.4.2.: "Interarticular protopodite muscles"; ERHARD 1995: 35).

M 52: The muscle is described as intrinsic levator (remotor) of the pleopod protopodite I in *Ligia oceanica* and is composed of numerous bundles (ERHARD 1995: 38). Comparable muscles are missing in the non-ligiidae Oniscidea (= Holoverticata, cf. ERHARD 1998b) and in *Metaphreatoicus.* However, a homology between M 52 of *Ligia* and M 47 of *Metaphreatoicus* and the Oniscidea-Holoverticata can't be excluded.

M 53: Arises on the mediobasal wall of the distal article of pleopod protopodite I and is inserted on the posterior sclerite between protopodite and exopodite I. Moves the sclerite in medioproximal direction and apparently works as stabilizer of the sclerite. Homologous to M 53 of the oniscid *Ligia oceanica* (cf. ERHARD 1995: 38).

Mm 54/55: Move the pleopod exopodite I in lateral direction. Composed of two distinct muscle bundles arising on the posterior wall of the distal article of protopodite I and inserting with one branch on the lateroposterior basis and with another branch on the lateroanterior basis of the exopodite I (cf. chapt. 4.4.2.: "Lateral exopodite locomotors"). Homologous to the muscles Mm 54 and 55 of the oniscid *Ligia oceanica* (ERHARD 1995: 37).

M 56: Arises on the posterior wall of the distal joint of pleopod protopodite I and is inserted together with M 53 on the posterior sclerite between protopodite and exopodite I. Moves the sclerite in proximal direction and, possibly, works as stabilizer of the sclerite. Presumably homologous to M 56 of *Ligia oceanica* (ERHARD 1995: 38). The homology of M 56 of *Metaphreatoicus* with M 50 of the Oniscidea-Orthogonopoda (= Mesoniscidae + Synocheta + Crinocheta), probably, might be right.

M 57: Locomotor of the pleopod exopodite I. Arises on the posterior sclerite between protopodite and exopodite I and is inserted on the anterior wall of the exopodite I. Composed of three bundles. Homologous to M 57 of the oniscid *Ligia oceanica* (cf. ERHARD 1995: 39).

M 115: Same funtion as M 51. Arises on the posterior side of the proximal proto-

podite I-article and is inserted laterally on the posterior wall of the distal joint of protopodite I. Composed of about three bundles.

M 116: Function? Arises on the posterior side of the proximal protopodite I-article and is inserted on the anterior wall of the distal protopodite I-article. Composed of one bundle.

M 117: Function? Arises on the medioanterior wall of the pleopod endopodite I-basis and is inserted on the lateroposterior side of the same region. Composed of about three bundles.

4.1.2. Comparison (figs. 4–7)

– M 117

In *Metaphreatoicus, Onchotelson, Pharamphisopus, Phreatoicopsis, Mesamphisopus* and presumably in *Nichollsia* an intrinsic pleopod endopodite I muscle M 117 is present. Within the Oniscidea, a homologous muscle is missing in the groups Ligiidae, Tylidae, Mesoniscidae and Synocheta. Only in the male Oniscidea-Crinocheta whose pleopod endopodite I is modified to a gonopod an intrinsic muscle M 49 occurs (Erhard 1995: 35). However, the hypothesis of a homology between the phreatoicidean muscle M 117 and M 49 of the Crinocheta seems to be questionable because it implies a reduction four times repeated in the oniscidean groups Ligiidae, Tylidae, Mesoniscidae and Synocheta (compare the phylogenetic relationships within the Oniscidea in Erhard 1997, 1998b). It appears to be more likely that the oniscidean groundpattern is lacking an intrinsic endopodite locomotor and the muscle M 49 in its special appearance has been developed in the stemline of the Crinocheta at the time when the male endopodite I was modified to a gonopod.

4.2. Pleopods II

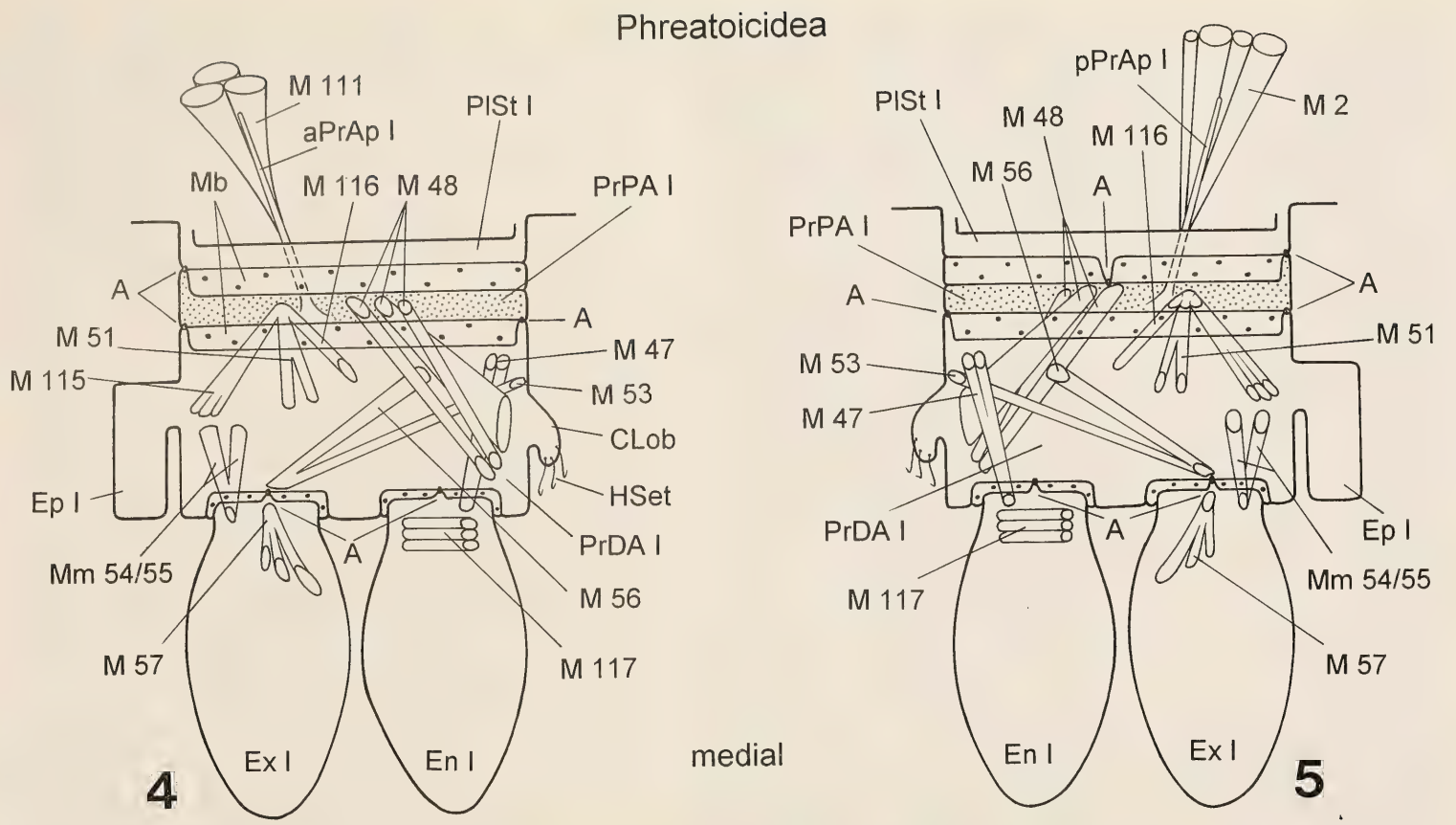
4.2.1 *Metaphreatoicus australis* (figs. 8–11)

4.2.1.1. Skeleton

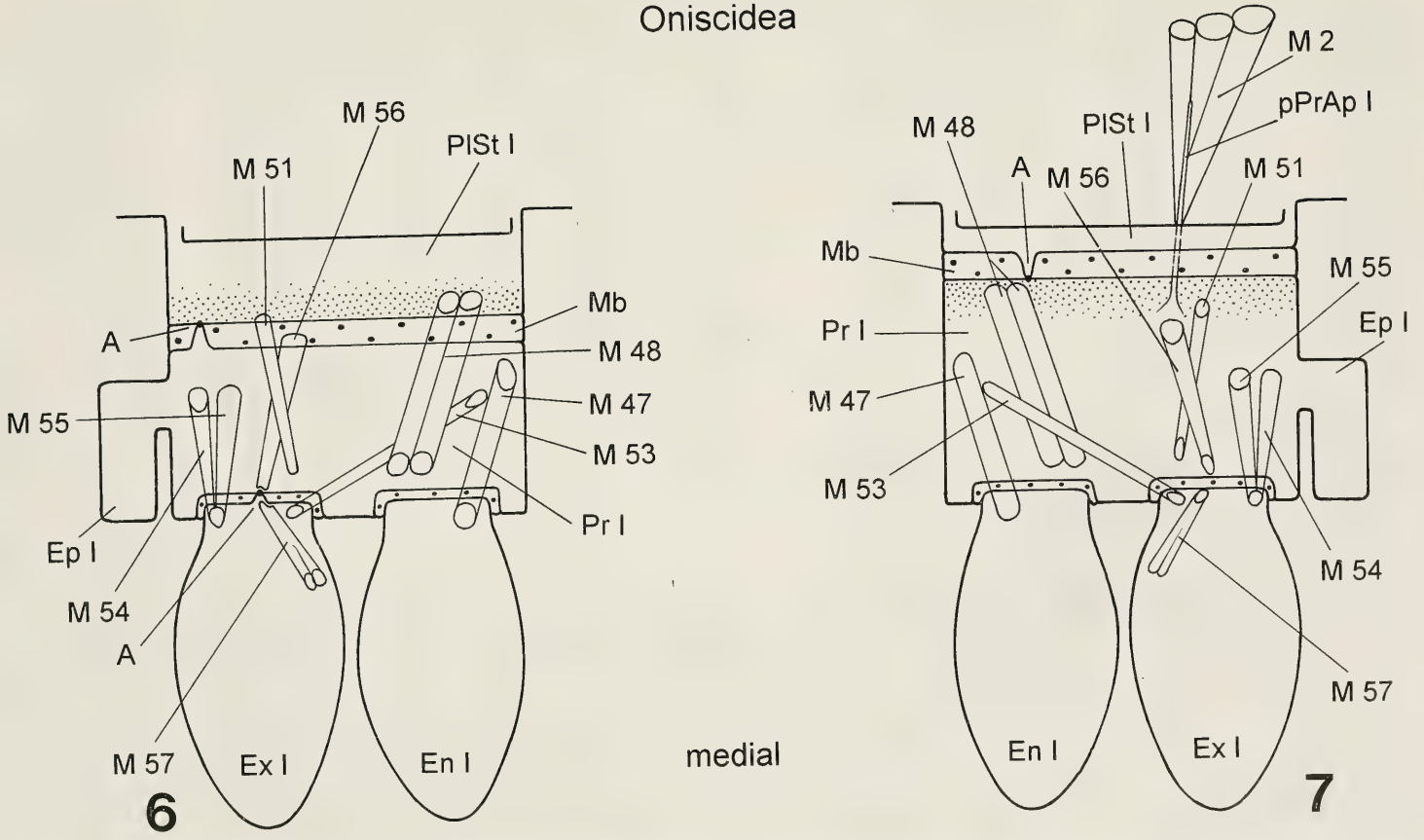
The male pleopod II of *Metaphreatoicus australis* is composed of a protopodite, an exo- and an endopodite whereas a lateral epipodite is missing.

As it is already described in detail for the pleopod I (cf. chapt. 4.1.1.1.), the pleopod protopodite II is composed of a short proximal joint and a large distal article. The articular points between sternite II and the proximal protopodite II-article are situated posteriorly and laterally, those between the proximal and distal protopodite joints are located medially and laterally (figs. 8–10; cf. chapt. 4.4.1: "Articulations of the pleopod protopodites"). The proximal article of protopodite II has two thin apophyses projecting dorsally into the pleon trunk (cf. Erhard 1998a: 12, fig. 4). The apophysis which arises at the anterior margin of the proximal protopodite joint serves as point of attachment for the extrinsic pleopod promotor M 5, and the posterior one as point of insertion for the extrinsic pleopod remotor M 6. The distal protopodite article has a small medial lobe bearing some long distally feathered setae which serve to couple with the opposite pleopod.

The male pleopod endopodite II is divided into two articles (figs. 9, 11). The protopodite and the proximal joint of the endopodite II have an articular point at the



Figs. 4–5. Diagrams of the skeleton and musculature of the pleopods I within the groundpattern of the Phreatoicidea. The pleopodal rami are projected onto the same level. Areas of the proximal protopodite articles indicated by *compact dotting*, membranes by *bold single dots*. – 4. Anterior view; – 5. posterior view.



Figs. 6–7. Diagrams of the skeleton and musculature of the pleopods I within the groundpattern of the Oniscidea. The pleopodal rami are projected onto the same level. Areas of the proximal protopodite articles indicated by *compact dotting*, membranes by *bold single dots*. – 6. Anterior view; – 7. posterior view.

posterior side. However, an anterior hinge could not be shown with certainty. Between the proximal endopodite II-article and the mediodistal joint (= appendix masculina) a dicondylic articulation is developed. It is formed by a posterior and an anterior articular point. The basal leaf-like endopodite joint is divided into a proximal sclerotized and a distal membranous region.

The distal part of the rodlike appendix masculina is curved laterally. The anterior wall of the joint is deepened along its length forming a channel which presumably serves for transporting of spermatophores to the female genital opening during copulation (fig. 11). At the sides of the trough short distally directed spines are developed which, probably, are guiding the spermatophores during their passage to the female gonopore. Presumably for the same purpose, the long hairs at the distal end of the appendix masculina are developed.

Between pleopod protopodite II and exopodite II a dicondylic articulation occurs which is quite similar to the corresponding condition within the pleopod I (figs. 8, 10; cf. chapt. 4.1.1.1.). The articular points are located anteriorly and posteriorly, the contact between protopodite II and exopodite II are formed by two sclerites. The pleopod exopodite II of *Metaphreatoicus* is composed of two joints with a narrow articulation inbetween. Locomotors of the distal exopodite article could not be shown. As in the pleopods III–V the basal joint of the exopodite II is equipped with medioproximal and lateroproximal lobes.

4.2.1.2. Musculature

Within this chapter information on the serial homology of the muscles in the pleopods I–III is added. An overview on the serial homologous muscles within the oniscidean pleon is given in ERHARD (1995: 96).

Mm 58/59: Intrinsic promotors of the pleopod protopodite II. Arise on an apophysis of the anterior wall of the proximal joint of the protopodite II, pass the membrane between the proximal and the distal protopodite joint and are inserted distally on the anterior wall of the distal protopodite II-article. Composed of two branches which are crossing each other. Homologous to the oniscidean muscles Mm 58/59 (cf. ERHARD 1995, 1996, 1997). Serial homologous to Mm 48 and 71/72 within the pleopods I and III.

M 60: The muscle present in the oniscidean groundpattern (ERHARD 1995: 58) is missing in *Metaphreatoicus australis* (cf. chapt. 4.2.2.: "Locomotors of the pleopod endopodite II").

M 61: Moves the endopodite II in medial direction. Arises medially on the basal wall of the distal protopodite II-article and is inserted on the medioposterior basis of the endopodite II. Composed of two muscle bundles. Homologous to the oniscidean muscle M 61 (cf. ERHARD 1995, 1996, 1997). Serial homologous to M 47 and M 73 (pleopods I and III) and to M 103 (uropods).

M 62: Locomotor of the mediodistal endopodite II-article (appendix masculina). On account of the oblique arrangement of the pleopods (cf. chapt. 4.4.1.), M 62 moves the appendix masculina in laterocranial direction. Arises on the medial wall of the proximal pleopod endopodite II-article and is inserted on a lateral apophysis of the appendix masculina. Composed of about 14 branches. Homologous to the oniscidean muscle M 62 (cf. ERHARD 1995, 1996, 1997).

M 63: Arises mediobasally on the distal article of pleopod protopodite II and is in-

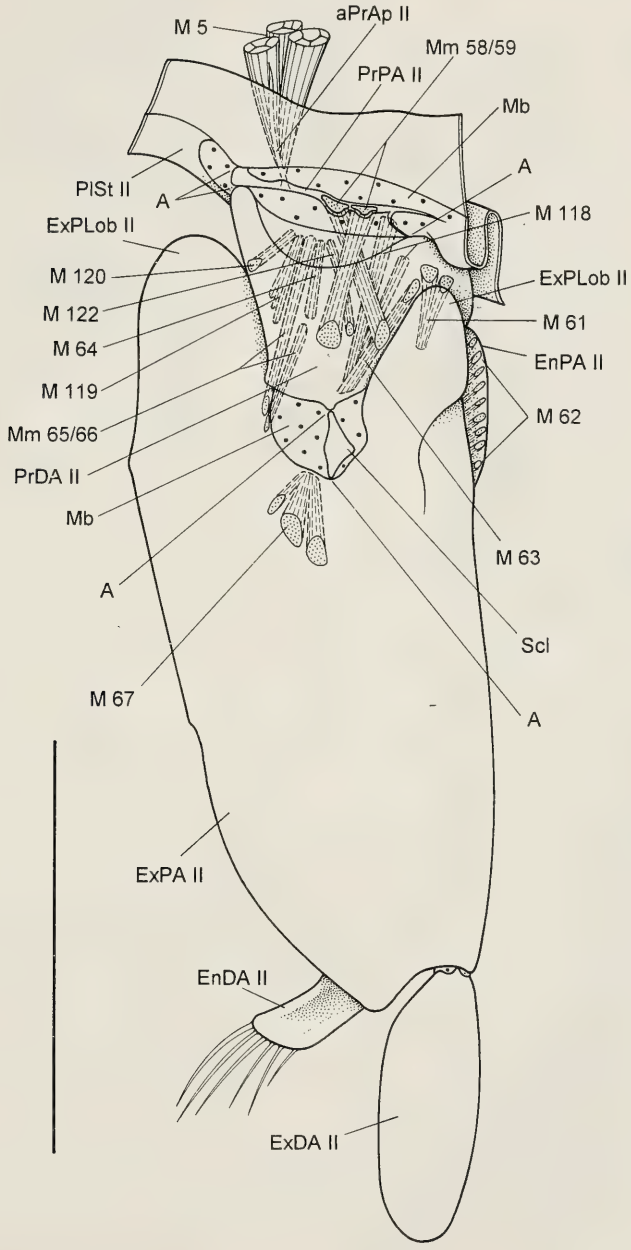


Fig. 8. *Metaphreatoicus australis*, ♂, right pleopod II in anterior view. – Scale: 1 mm.

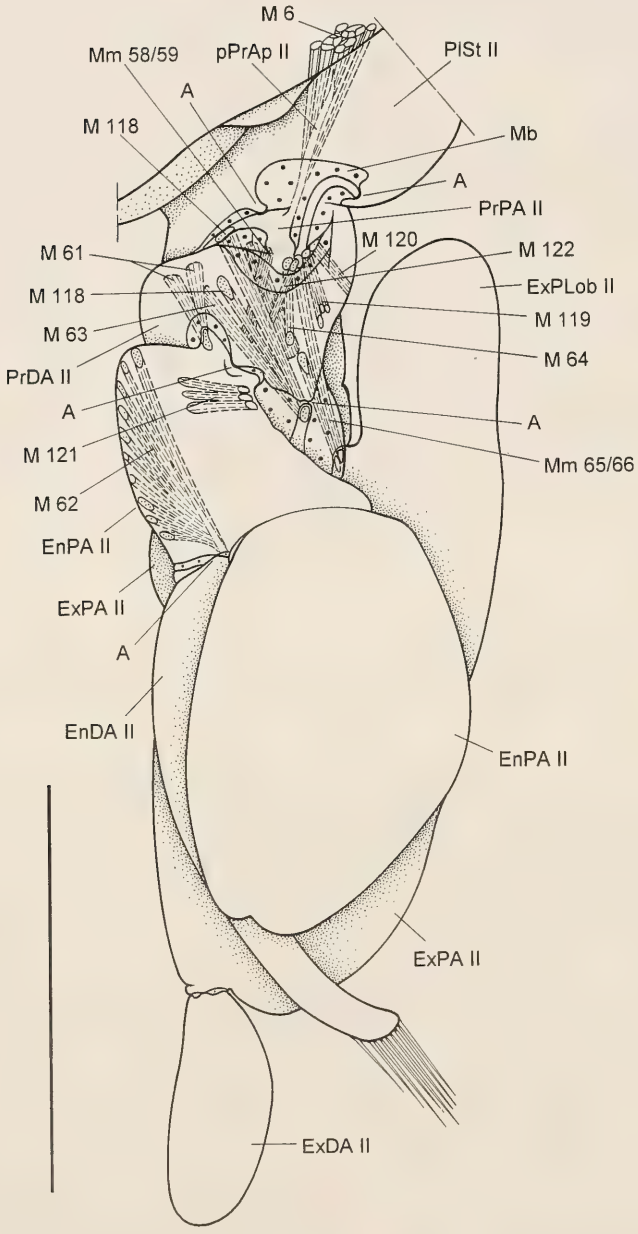
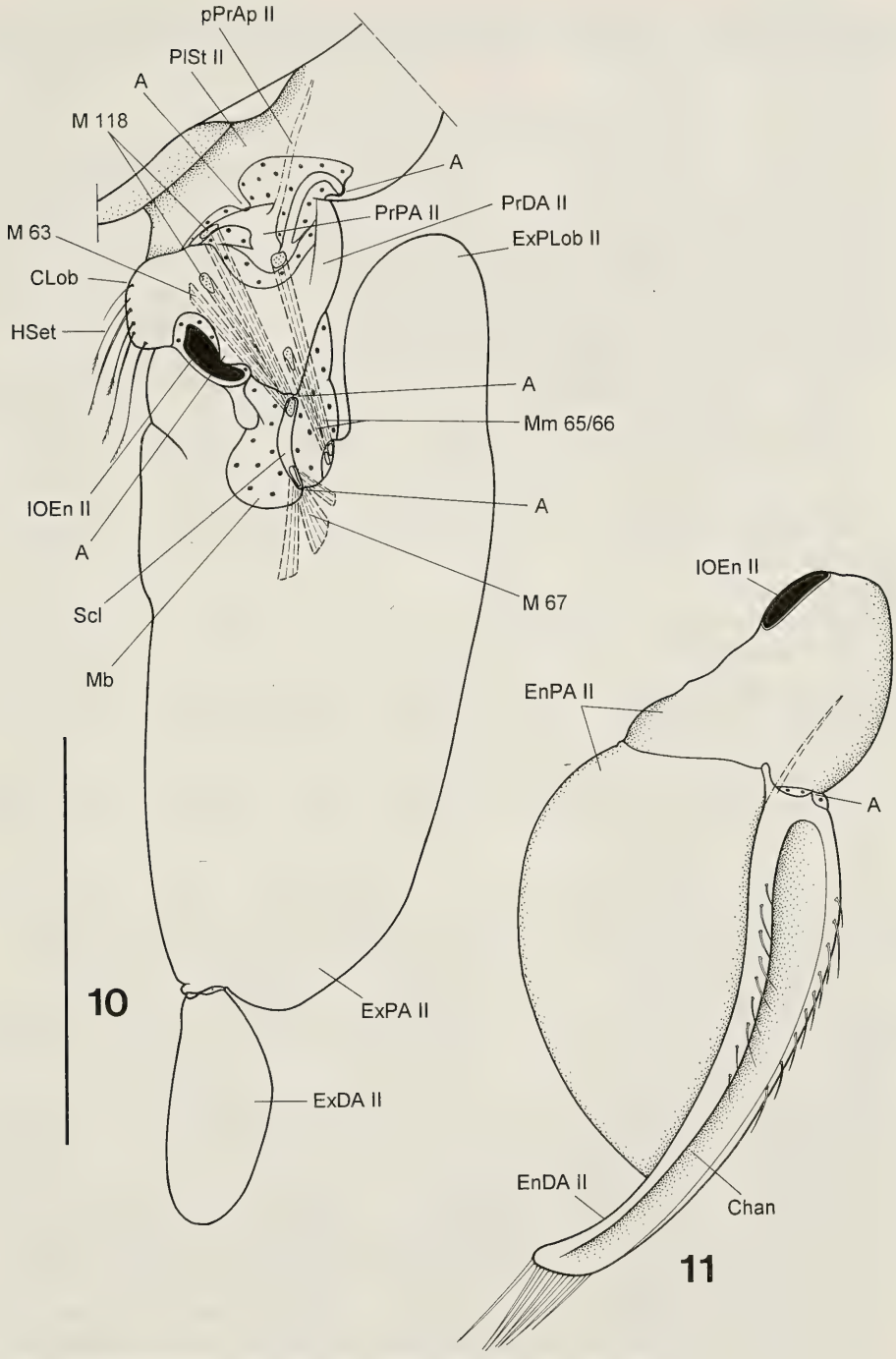


Fig. 9. *Metaphreatoicus australis*, ♂, right pleopod II in posterior view. – Scale: 1 mm.



Figs. 10–11. *Metaphreatoicus australis*, ♂. – 10. Right pleopod II in posterior view. Endopodite and musculature except for the exopodite locomotors removed. – 11. Right pleopod endopodite II in anterior view. – Scale: 1 mm.

serted together with M 118 on the posterior sclerite between protopodite and exopodite II. Moves the sclerite in medioproximal direction. Presumably, homologous to the oniscidean muscle M 63. Serial homologous to M 53 (cf. chapt. 4.4.2.: "Medial exopodite locomotors").

M 64: Presumably, the muscle is transmissing the power of the extrinsic pleopod II-remotor M 6, which is inserted on the remotor apophysis at the posterior side of the proximal protopodite II-article (cf. ERHARD 1998a: 32), to the distal joint of pleopod protopodite II. Arises on the posterior side of the proximal protopodite II-article and is inserted on the lateroposterior wall of the distal joint of protopodite II. On account of its pass, the muscle, probably, might be homologous to the oniscidean muscle M 64 retained in the Oniscidea-Crinocheta (cf. ERHARD 1995). Serial homologous to M 51 and M 75 within the pleopods I and III.

Mm 65/66: Move the pleopod exopodite II in lateral direction. Composed of two distinct muscle bundles. One branch arises on the posterior wall of the distal article of the protopodite II and is inserted on the lateroposterior basis of the exopodite II. The second branch arises on the posterior side of the proximal protopodite II-article and is inserted on the lateroanterior basis of the exopodite II (cf. chapt. 4.4.2.: "Lateral exopodite locomotors"). Homologous to the oniscidean muscles Mm 65 and 66 (cf. ERHARD 1995). Serial homologous to Mm 54/55 and 77/78 within the pleopods I and III.

M 67: Locomotor of the pleopod exopodite II. Arises distally on the posterior sclerite between protopodite II and exopodite II and is inserted on the anterior wall of the proximal exopodite II-article. Composed of three bundles. Homologous to the oniscidean muscle M 67 (cf. ERHARD 1995, 1996, 1997). Serial homologous to M 57 and M 80 within the pleopods I and III.

M 68: The muscle which is present in the pleopod protopodite II of the oniscid *Ligia oceanica* (ERHARD 1995: 49) could not be found in *Metaphreatoicus australis* (cf. chapt. 4.4.2.: "Mm 116, 122, 123").

M 118: Arises with a medial small bundle on the posterior wall of the distal article of protopodite II and with a lateral strong branch on the posterior side of the proximal protopodite II-article. M 118 is inserted together with M 63 on the posterior sclerite between protopodite II and exopodite II. Moves the sclerite in proximal direction and possibly works as stabilizer of the sclerite. Serial homologous to M 56 and M 79 within the pleopods I and III (cf. chapt. 4.4.2.: "Medial exopodite locomotors").

M 119: Same function as M 64. Arises posteriorly on the proximal pleopod protopodite II-article and is inserted laterally on the posterior wall of the distal joint of protopodite II. Composed of about three bundles. Serial homologous to parts of M 115 (pleopod I) and to M 124 (pleopod III).

M 120: Same function as M 64. Arises posteriorly on the proximal pleopod protopodite II-article and is inserted anteriolaterally on the distal joint of pleopod protopodite II. Composed of one bundle. Serial homologous to parts of M 115 (pleopod I) and to M 125 (pleopod III).

M 121: Function? Arises on the medioanterior wall of the basal part of the pleopod endopodite II and is inserted on the lateroposterior wall of the same article. Composed of about three bundles. Serial homologous to M 117 and M 126 within the pleopods I and III.

M 122: Function? Arises posteriorly on the proximal protopodite II-article and is

inserted on the anterior side of the distal joint of protopodite II nearby the points of insertion of Mm 58/59. Serial homologous to M 116 and M 123 within the pleopods I and III.

4.2.2. Comparison (figs. 12–16)

– Articles of the pleopod endopodite II

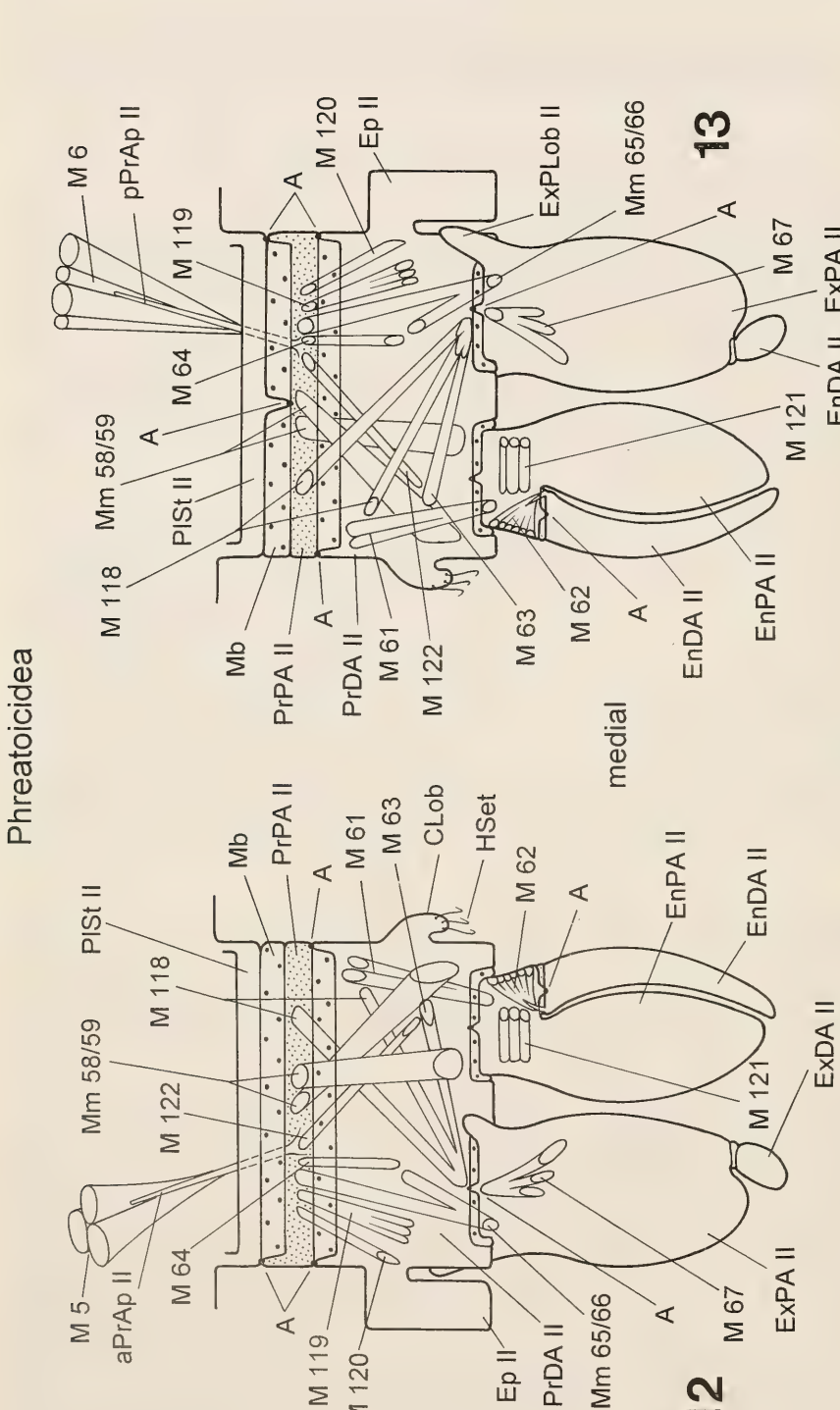
In the case of the male phreatoicidean specimens the pleopod endopodite II is divided into the mediodistal appendix masculina and the proximal leaf-like joint. Corresponding to the ontogenetical development of the appendices masculinae of *Sphaeroma hookeri* (Sphaeromatidae) reported by KINNE (1954) the rodlike appendix is formed by a mediodistal part of the proximal endopodite II-article. The distal part of this leaf-like joint of the male endopodite II is retained in the Phreatoicidea. In the Oniscidea only the basal part of the formerly leaf-like joint is retained while the distal region is completely reduced which might represent an apomorphous character state.

– Articulation between the endopodite II-articles

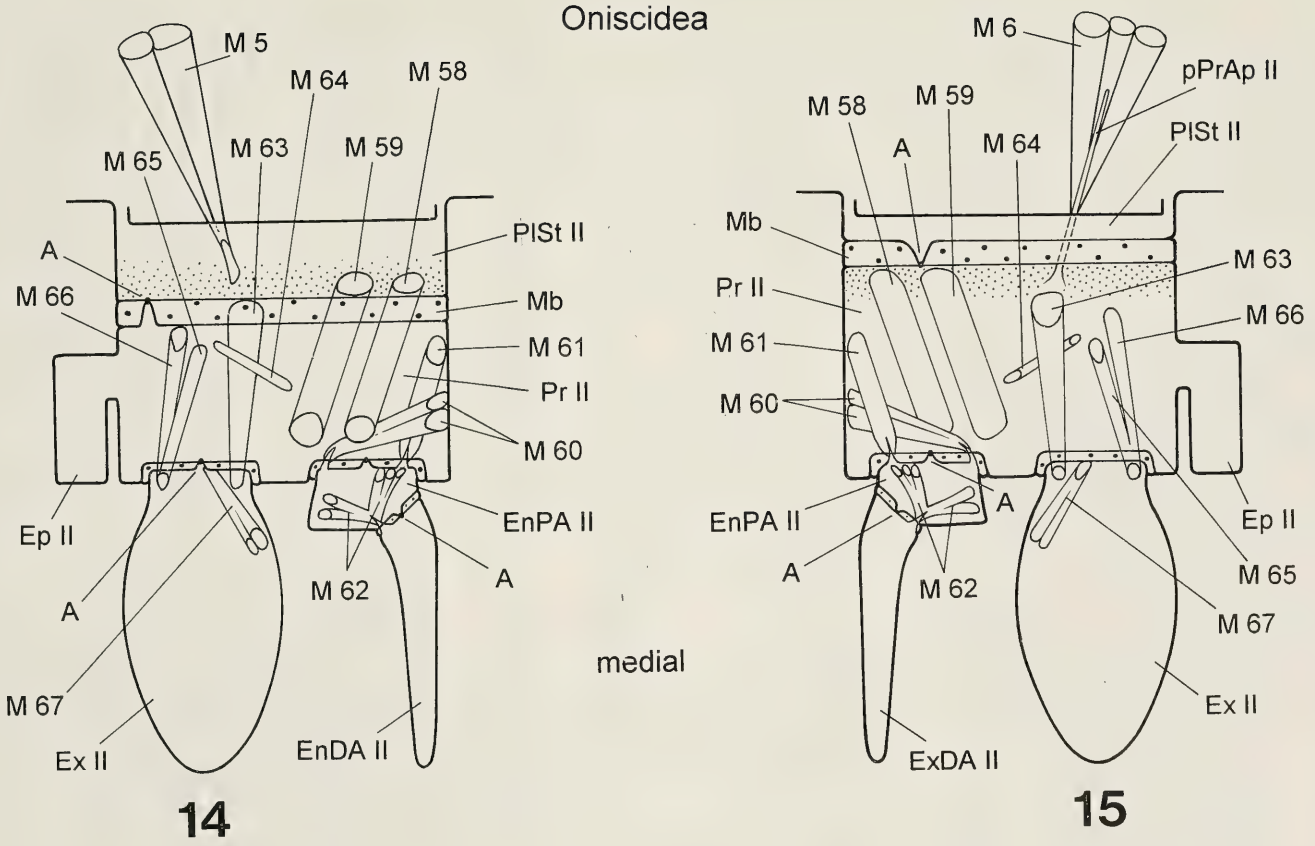
Between the proximal endopodite II-joint and the mediodistal article (appendix masculina) in *Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* as well as in the oniscidean groundpattern a dicondylic articulation is present. In subordinate oniscidean taxa (Tylidae, Mesoniscidae) monocondylic articulations occur (cf. ERHARD 1997: 43).
In *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus* and *Phreatoicopsis* the appendix masculina is inserted proximally on the proximal article of the pleopod endopodite II (fig. 11). In contrast, in *Nichollsia* and *Mesamphisopus* the gonopod seems to be shifted distally and is inserted approximately at half the length of the medial wall of the proximal endopodite II-article (fig. 16; TIWARI 1950: pl. 20, fig. 2; NICHOLLS 1943: fig. 9, 11).

– Shape of the appendix masculina

In the investigated genera *Metaphreatoicus, Colubotelson, Paramphisopus* and *Phreatoicopsis* the appendix masculina is curved laterally. Therefore, a functional co-operation by the distal parts of the appendices of both sides during copulation, probably, has not to be supposed because of the spatial distance of both regions.
In male specimens fo *Nichollsia kashiensis* the appendix is also curved laterally. However, the penial stylet represents a complex organ which is supposed to be a derived feature in respect to the appendices masculinae within the phreatoicidean and isopodan groundpatterns. The distal region of the gonopod in *Nichollsia* is transformed to a whip-like sclerotized thread which is rolled up at least in fixed specimens to a loop of about 360° (fig. 16). The basal part of the appendix is fixed by a membrane to the adjacent region of the leaf-like endopodite II area. The free distal whip-like part of the appendix might be moved in distal direction by contraction of the gonopod locomotor M 62. This peculiar shape of the appendix masculina was described incorrectly by CHOPRA & TIWARI (1950: pl. 20, fig. 2) and GUPTA (1989: figs. 6–7) because the whip-like distal part of the appendix was overseen. However, this fragile distal part may easily break off.
In *Mesamphisopus capensis* and *Onchotelson brevicaudatus* the distal region of the appendix is curved only slightly in lateral direction. Within the oniscidean groundpattern both appendices masculinae (= distal articles of male pleopod en-



Figs. 12–13. Diagrams of the skeleton and musculature of the pleopods II within the groundpattern of the Phreatoicidea. Pleopodal rami projected onto the same level. Areas of the proximal protopodite articles indicated by *compact dotting*, membranes by *bold single dots*. – 12. Anterior view; – 13. posterior view.



Figs. 14–15. Diagrams of the skeleton and musculature of the pleopods II within the groundpattern of the Oniscidea. Pleopodal rami projected onto the same level. Areas of the proximal protopodite articles indicated by *compact dotting*, membranes by *bold single dots*. – 14. Anterior view; – 15. posterior view.

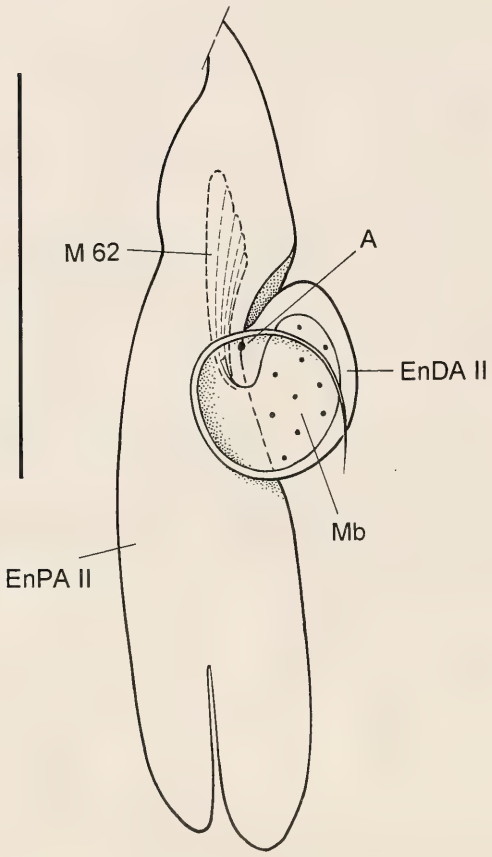


Fig. 16. *Nichollsia kashiensis*, ♂, right pleopod endopodite II in anterior view, in vitro. – Scale: 1 mm.

dopodite II) have linear shapes and are positioned in the midventral region of the pleon ventrum side by side or one upon another (Erhard 1996: 23). Thus, they are able to work together during copulation for the purpose of sperm transport to the female gonopore. Like most phreatoicideans the isopodan incertae sedis group *Tainisopus* shows laterally curved appendices masculinae.

– Channel of the appendix masculina

In *Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and in the incertae sedis group *Tainisopus* (Wilson & Keable, in press) as well as in the groundpattern of the Oniscidea the anterior wall of the appendix masculina (= distal pleopod endopodite II-article of the Oniscidea) is deepened and is forming a groove for the distally directed transport of spermatophores during copulation (Erhard 1996: 22). Within the Oniscidea-Holovertica-ta (= Tylidae + Mesoniscidae + Synocheta + Crinocheta, cf. Erhard 1998b: 304) the channel is present at the medial wall of the appendix. Together with the channel of the corresponding limb of the opposite side it is forming a closed sperm duct. The latter character state represents an apomorphous feature in respect to the isopodan and oniscidean groundpatterns (Erhard 1997: 47, 1998b: 304). In

contrast to the described phreatoicidean condition, a groove at the derived whip-like appendix masculina of *Nichollsia kashiensis* (cf. preceding paragraph, fig. 16) could not be shown.

– Locomotors of the pleopod endopodite II Mm 60 and 61

In the oniscidean groundpattern two distinct locomotors of the pleopod endopodite II are present, inserting on the medial (M 61) and the lateral (M 60) endopodite basis (ERHARD 1995, 1996, 1997). In *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* only the medial locomotor M 61 is developed. A comparable situation with only one endopodite locomotor occurs within the pleopods I, III–V and the uropods of the Phreatoicidea as well as in the pleopods I, III–V and the uropods within the oniscidean groundpattern (ERHARD 1995). This pattern of character states reveals the existence of an additional lateral endopodite locomotor M 60 inside the oniscidean pleopod II to be an apomorphous condition in comparison with the phreatoicidean and, presumably, the isopodan groundpattern.

– Locomotor of the appendix masculina M 62

In *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* as well as in the Oniscidea (ERHARD 1995, 1996, 1997) the mediodistal article of the male pleopod endopodite II (appendix masculina) is moved by the muscle M 62. The presence of this muscle is assumed to be a groundpattern character of the Phreatoicidea and Oniscidea.

4.3. Pleopods III

4.3.1. *Metaphreatoicus australis* (figs. 17–19)

4.3.1.1. Skeleton

The male pleopod III of *Metaphreatoicus australis* consists of a protopodite, an exo- and an endopodite. In contrast to the pleopods I and II, the pleopod protopodites III–V bear lateral epipodites.

The pleopod protopodite III is composed of a short proximal and a large distal article. The articular points between sternite III and the proximal protopodite III-article are situated posteriorly and laterally, those between the proximal and distal protopodite joints are located medially and laterally. As in the other pleopods, the proximal article of protopodite III has two thin apophyses projecting dorsally into the pleon trunk (cf. ERHARD 1998a: 12 and figs. 4, 13–15). The apophysis which arises from the anterior margin of the proximal protopodite joint (fig. 17) serves as point of attachment for the extrinsic pleopod promotor M 112, and the posterior one (figs. 18–19) as point of insertion for the extrinsic pleopod remotor M 9. The lateral epipodite is inserted on the distal protopodite article. On the medial side of this distal protopodite joint a nose-like lobe is developed which bears distally feathered coupling hairs (fig. 18). A corresponding structure is also present in the pleopods II and IV–V but is missing in the pleopods I.

Between protopodite III and endopodite III a posterior articular point is developed. An anterior hinge could not be shown with certainty. The endopodite III is composed of a short sclerotized proximal area and a distal leaf-like membranous region (fig. 18).

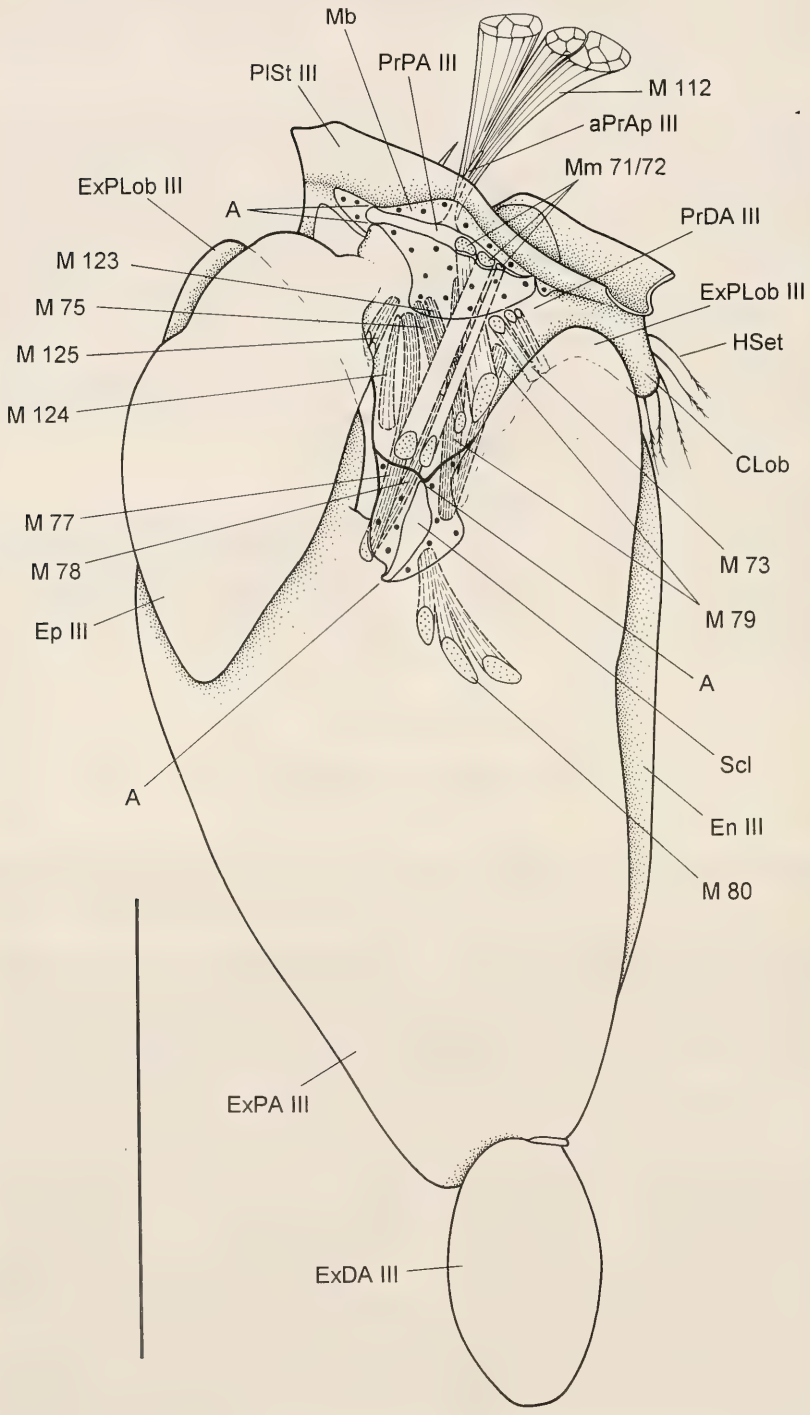


Fig. 17. *Metaphreatoicus australis*, ♂, right pleopod III in anterior view. – Scale: 1 mm.

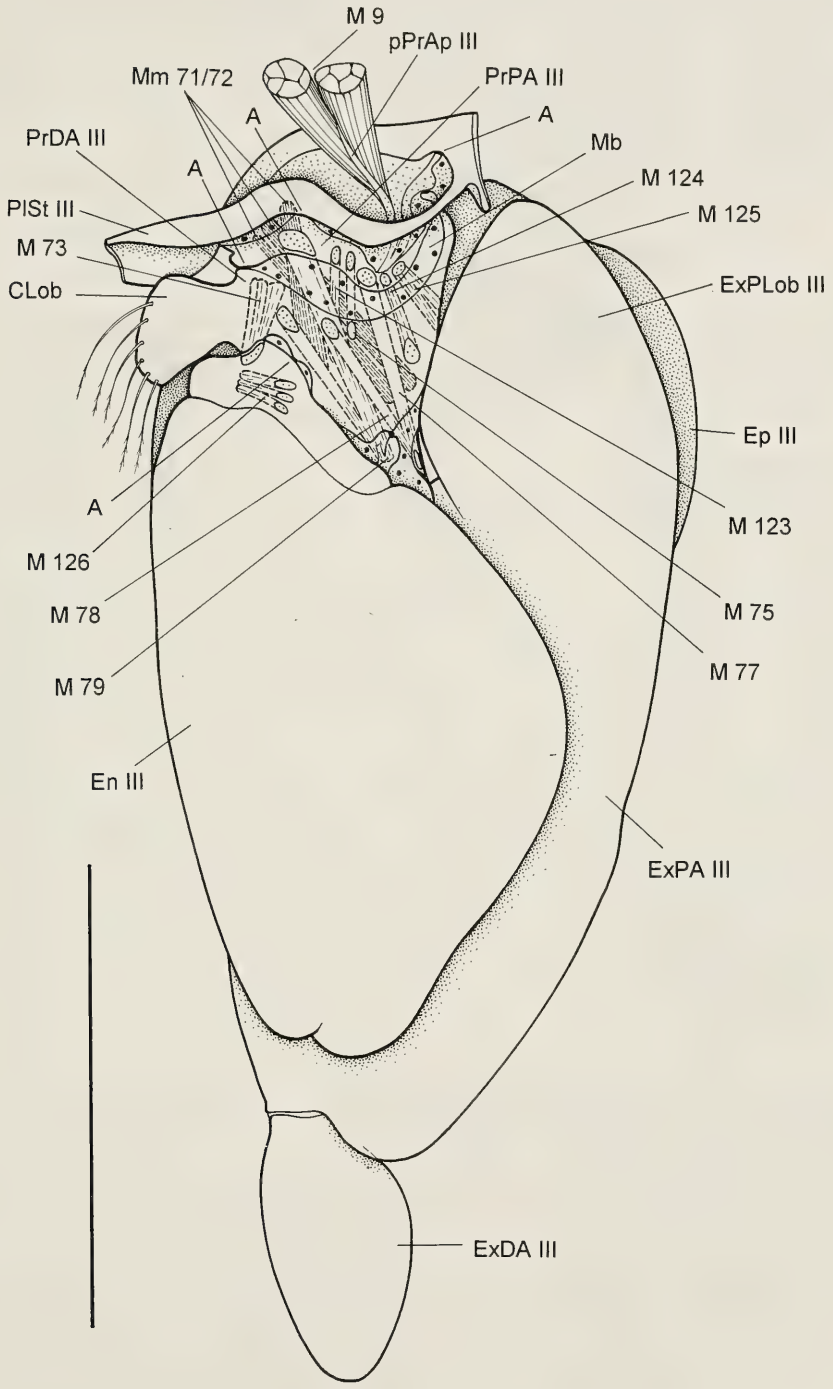


Fig. 18. *Metaphreatoicus australis*, ♂, right pleopod III in posterior view. – Scale: 1 mm.

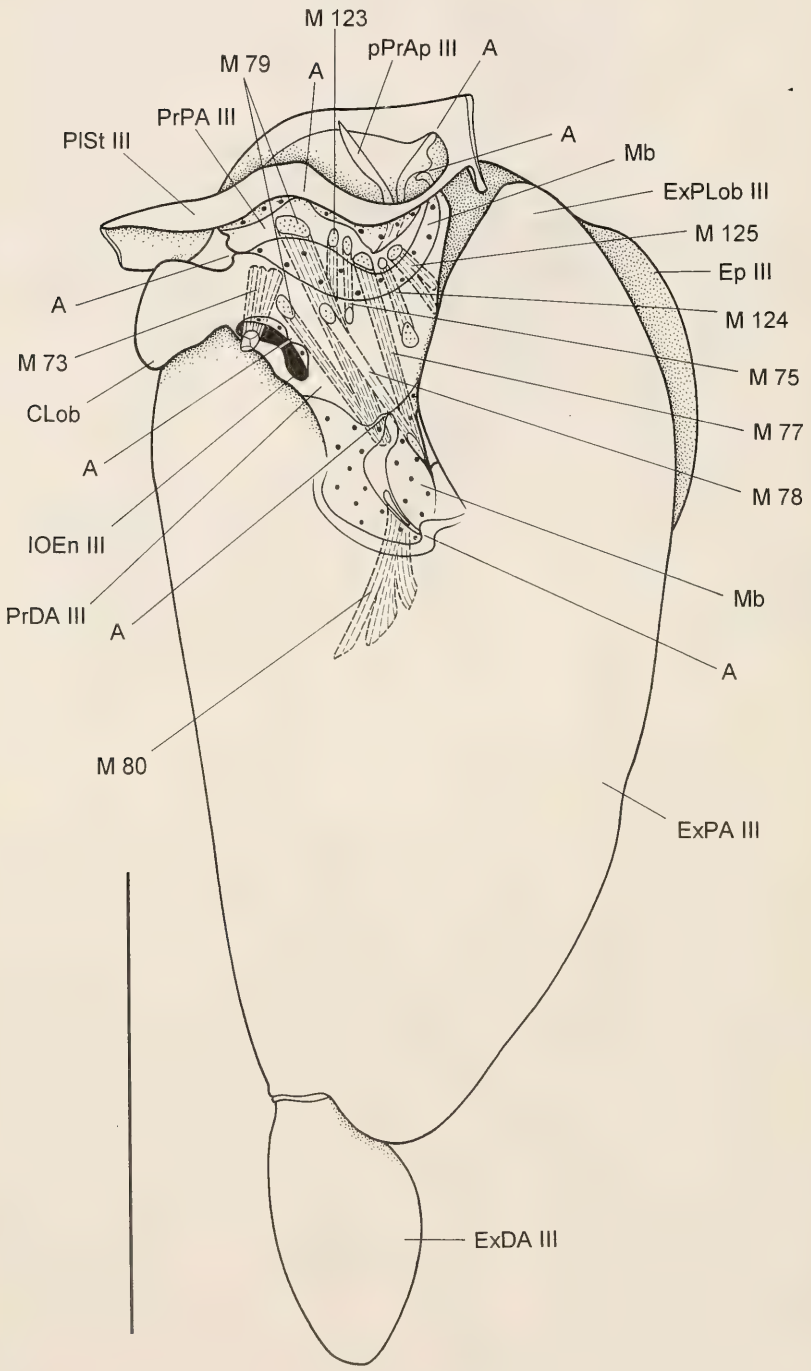


Fig. 19. *Metaphreatoicus australis*, ♂, right pleopod III in posterior view. Endopodite, coupling setae as well as the muscles Mm 9 and 71/72 removed. – Scale: 1 mm.

The pleopod protopodite III and the exopodite III have a dicondylic articulation. As in the pleopods I and II the articular points are located anteriorly and posteriorly, the articular contact between protopodite III and exopodite III are formed by two sclerites (figs. 17, 19). The pleopod exopodite III of *Metaphreatoicus* is composed of two articles with a narrow articulation between them. However, distinct articular points between the proximal and distal exopodite article could not be shown. As in the pleopods II and IV–V the basal joint of the exopodite III has medioproximal and lateroproximal lobes (fig. 17: ExPLob III).

4.3.1.2. Musculature

Mm 71/72: Intrinsic promotors of the pleopod protopodite III. Arise on the anterior wall of the proximal joint of the protopodite III, pass the membrane between the proximal and the distal protopodite joint and are inserted distally on the anterior wall of the distal protopodite III-article. Composed of three bundles which are crossing each other. Homologous to the oniscidean muscles Mm 71/72 (cf. ERHARD 1995, 1996, 1997).

M 73: Moves the endopodite III in medial direction. Arises medially on the basal wall of the distal protopodite III-article and is inserted on the medioposterior basis of the endopodite III. Composed of three muscle bundles. Homologous to the oniscidean muscle M 73 (cf. ERHARD 1995, 1996, 1997).

M 75: Presumably, the muscle is transmissing the power of the extrinsic pleopod III-remotor M 9 to the distal protopodite III-article. Arises on the posterior side of the proximal protopodite III-article and is inserted on the posterior wall of the distal joint of protopodite III. On account of its pass, the muscle, probably, is homologous to the oniscidean muscle M 75 (cf. ERHARD 1995).

M 76: The medial pleopod exopodite III-locomōtor M 76 present in the Oniscidea (ERHARD 1995, 1996, 1997) could not be found with certainty in *Metaphreatoicus australis* (cf. chapt. 4.4.2.: "Medial exopodite locomotors").

Mm 77/78: Move the pleopod exopodite III in lateral direction. Composed of two distinct muscle bundles. One branch arises on the posterior wall of the distal article of the protopodite III and is inserted on the lateroposterior basis of the exopodite III. The other branch arises on the posterior side of the proximal protopodite III-article and is inserted on the lateroanterior basis of the exopodite III (cf. chapt. 4.4.2: "Lateral exopodite locomotors"). Homologous to the oniscidean muscles Mm 77 and 78 (cf. ERHARD 1995, 1996, 1997).

M 79: Arises with a medial small bundle on the posterior wall of the distal article of protopodite III and with a lateral strong branch on the posterior side of the proximal protopodite III-article. M 79 is inserted on the posterior sclerite between protopodite III and exopodite III. Moves the sclerite in proximal direction. Homologous to the oniscidean muscle M 79 present in *Ligia oceanica* (cf. ERHARD 1995: 62).

M 80: Locomotor of the pleopod exopodite III. Arises distally on the posterior sclerite between protopodite III and exopodite III and is inserted on the anterior wall of the proximal exopodite III-article. Composed of three bundles. Homologous to the oniscidean muscle M 80 (cf. ERHARD 1995, 1996, 1997).

M 123: Function? Arises posteriorly on the proximal protopodite III-article and is inserted on the anterior side of the distal joint of protopodite III nearby the points of insertion of Mm 71/72.

M 124: Same function as M 75. Arises posteriorly on the proximal pleopod proto-

podite III-article and is inserted laterally on the posterior wall of the distal joint of pleopod protopodite III. Composed of one bundle.

M 125: Same function as M 75. Arises posteriorly on the proximal pleopod protopodite III-article and is inserted anteriolaterally on the distal joint of pleopod protopodite III. Composed of two bundles.

M 126: Function? Arises on the medioanterior wall of the basal part of the pleopod endopodite III and is inserted on the lateroposterior wall of the same region. Composed of about three bundles.

4.4. Comparison of characters concerning all pleopods (figs. 4–7, 12–15, 20–23)

4.4.1 Skeleton

Concerning the internal and external anatomy the pleopods IV and V differ only slightly from the pleopods III in most isopod groups. Therefore, the morphological description of the pleopods III can be applied largely to the pleopods IV and V. Concerning the numbering of the muscles within these limbs it is referred to the description of the pleopods IV and V in *Oniscus asellus* and to an overview on the serial homologous muscles within the oniscidean pleon given by Erhard (1995: 72, 96).

– Orientation of the pleopod rami

In *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus* the flat sides of the pleopod endo- and exopodites are not orientated strictly to the transversal plane of the body but are slightly turned to the sagittal plane. Their medial margins are directed mediocaudally and their lateral margins laterocranially. This orientation causes an oblique arrangement of all five pairs of pleopods (cf. Erhard 1998a: fig. 2). In contrast, in the Oniscidea (cf. Erhard 1995: figs. 3, 8, 10) and in *Nichollsia kashiensis* the medial margins of the pleopod rami are directed medially or mediocranially.

– Protopodite joints

On the proximal pleopod protopodite sclerites (figs. 4–5, 12–13, 20–21: PrBa) of *Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* which are interposing between the pleonal sternites and the distal protopodite parts, muscles like the intrinsic and extrinsic pleopod promotors are attached. The oniscidean homologous muscles have their origin on the anterior parts of the pleon sternites (figs. 6–7, 14–15, 22–23: PlSt; cf. Erhard 1995, 1996, 1997). Another situation applies to the apophyses of the extrinsic pleopod remotors which have their origin on the posterior walls of the proximal protopodite sclerites in *Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* (figs. 5, 13, 21) and in the Oniscidea on the posterior protopodite walls (figs. 7, 15, 23). Furthermore, intermediate sclerites between sternites and protopodites are missing in the Oniscidea but occur within the Phreatoicidea. Finally, the interarticular protopodite muscles Mm 115, 119/120 and 124/125, which are stretched between the proximal sclerites and the distal protopodite regions, still are present in phreatoicidean species but are missing in the Oniscidea (cf. chapt. 4.4.2.: "Interarticular protopodite muscles").

On account of these findings it has to be assumed that the intermediate sclerites of the pleopods in phreatoicidean species represent proximal protopodite joints. Corresponding sclerites of the oniscidean ancestors must have fused completely with the pleon sternites (concerning the anterior sides) or with the distal protopodite joints (concerning the posterior sides) during evolution of terrestrial isopods. The occurence of two or three joints of the pleopod protopodites in the Isopoda (e.g. *Bathynomus, Sphaeromides, Cirolana, Aega, Arcturus*) or other malacostracan groups (cf. HANSEN 1925, ZIMMER 1927, GRUNER 1993) is interpreted in general as an ancestral condition within the Malacostraca. This would explain the character state present in the investigated phreatoicidean species to be plesiomorphous in comparison with the apomorphous situation of the Oniscidea.

– Articulations of the pleopod protopodites

In *Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* the articular points between pleonal sternites and pleopod protopodites are situated posteriorly and laterally. Between the proximal and distal protopodite joints the articular points are positioned laterally and medially (figs. 4–5, 12–13, 20–21). Working on the assumption that in the oniscidean ancestors the proximal protopodite joint fused posteriorly with the distal protopodite article and anteriorly with the sternite (see preceding paragraph), posterior and lateral articular points between sternites and protopodites were resulting. Indeed, within the oniscidean groundpattern anteriolateral and posteriomedial articular points between sternites and protopodites are present (figs. 6–7, 14–15, 22–23; ERHARD 1995: 72).

– Articulation between pleopod protopodites and endopodites

Between the male pleopod protopodites and endopodites I–V of *Metaphreatoicus, Onchotelson* and *Nichollsia* posterior articular points are developed. However, anterior hinges could not be shown with certainty. In contrast, in the pleopods I–V of *Colubotelson, Phreatoicopsis* and *Mesamphisopus* and at least in the pleopods II–V of *Paramphisopus* dicondylic articulations between male protopodites and endopodites are present with posterior and anterior hinges (figs. 4–5, 12–13, 20–21). A corresponding dicondylic articulation occurs also in male pleopods II within the oniscidean groundpattern (figs. 14–15; ERHARD 1995: 58). However, articular points between the protopodites and endopodites of the pleopods III–V are missing in the Oniscidea because the bases of the endopodites are no longer sclerotized (figs. 6–7, 22–23; ERHARD 1995, 1996, 1997) as it is still the case in all investigated phreatoicidean species.

Distinct hinges could be determined between pleopod protopodites I and endopodites I of those male oniscidean species which are using the pleopod endopodites I for sexual purposes (cf. ERHARD 1995, 1997). However, the modification of male endopodites I to gonopods describes an apomorphous feature within the subordinate oniscidean groups Synocheta and Crinocheta which, presumably, concerns also the type of articulation of the corresponding limbs. In oniscidean species whose male endopodites I are not specialized as gonopods distinct hinges could not be shown (e.g. Ligiidae, Mesoniscidae, cf. ERHARD 1995, 1996).

At the present state of knowledge, the pattern of characters might be interpreted in this way that the existence of a dicondylic articulation between the pleopod protopodites and endopodites I–V represents the plesiomorphous condition in

respect to the isopodan groundpattern. This plesiomorphous situation then might be retained in the phreatoicidean groundpattern of all pleopods as well as in the male pleopods II of the Oniscidea (figs. 4–5, 12–15, 20–21). A reduction of articular points between protopodites and endopodites on account of the lack of sclerotized endopodite bases then has to be interpreted as an apomorphous character state which is present in the oniscidean pleopods III–V (figs. 22–23).

– Articulations between pleopod protopodites and exopodites

Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus and *Nichollsia* have dicondylic articulations between protopodites and exopodites of all pleopods (figs. 4–5, 12–13, 20–21). In the Oniscidea dicondylic articulations between protopodites and exopodites of the pleopods III–V are present in the groups Tylidae, Mesoniscidae and Crinocheta whereas *Ligia oceanica* (Ligiidae) and *Titanethes albus* (Synocheta) have only one articular point respectively (Erhard 1995, 1996, 1997).

Important for the character analysis seems to be the occurence of monocondylic articulations between proto-and exopodites of the pleopods I and II in all oniscidean species investigated so far and thus within the oniscidean groundpattern (figs. 6–7, 14–15; cf. Erhard 1995, 1996, 1997). On account of the dicondylic articulation in the pleopods I–V within the outgroup Phreatoicidea and the presumable retention of the dicondylic articulation in the pleopods III–V in the groundpattern of the Oniscidea-Holoverticata (= Tylidae + Mesoniscidae + Synocheta + Crinocheta, cf. Erhard 1998b) it has to be assumed that the presence of monocondylic articulations between proto- and exopodites of oniscidean pleopods represents an apomorphous feature in relation to the isopodan groundpattern.

– Guiding lobes for the pleopod exopodites III–V

In all oniscidean species investigated so far the pleopod protopodites III–V have posterior sclerotized lobes which probably are guiding the exopodites III–V during their movements ("Führungslappen" according to Erhard 1995, 1996, 1997). As far as posterior articular points between protopodites and exopodites III–V are developed (Tylidae, Mesoniscidae, Crinocheta), the guiding lobes are situated medially to these (cf. Erhard 1995: figs. 58–72). In contrast, in *Metaphreatoicus, Colubotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* sclerotized guiding lobes are missing for all pleopod exopodites. Provided that the pleopods I–V of the Phreatoicidea and the pleopods I and II of the Oniscidea show the plesiomorphous condition without exopodite guiding lobes, the development of these structures might represent an apomorphous character state of the Oniscidea. However, further anatomical comparisons are necessary to make clear statements.

– Articles of the pleopod exopodites

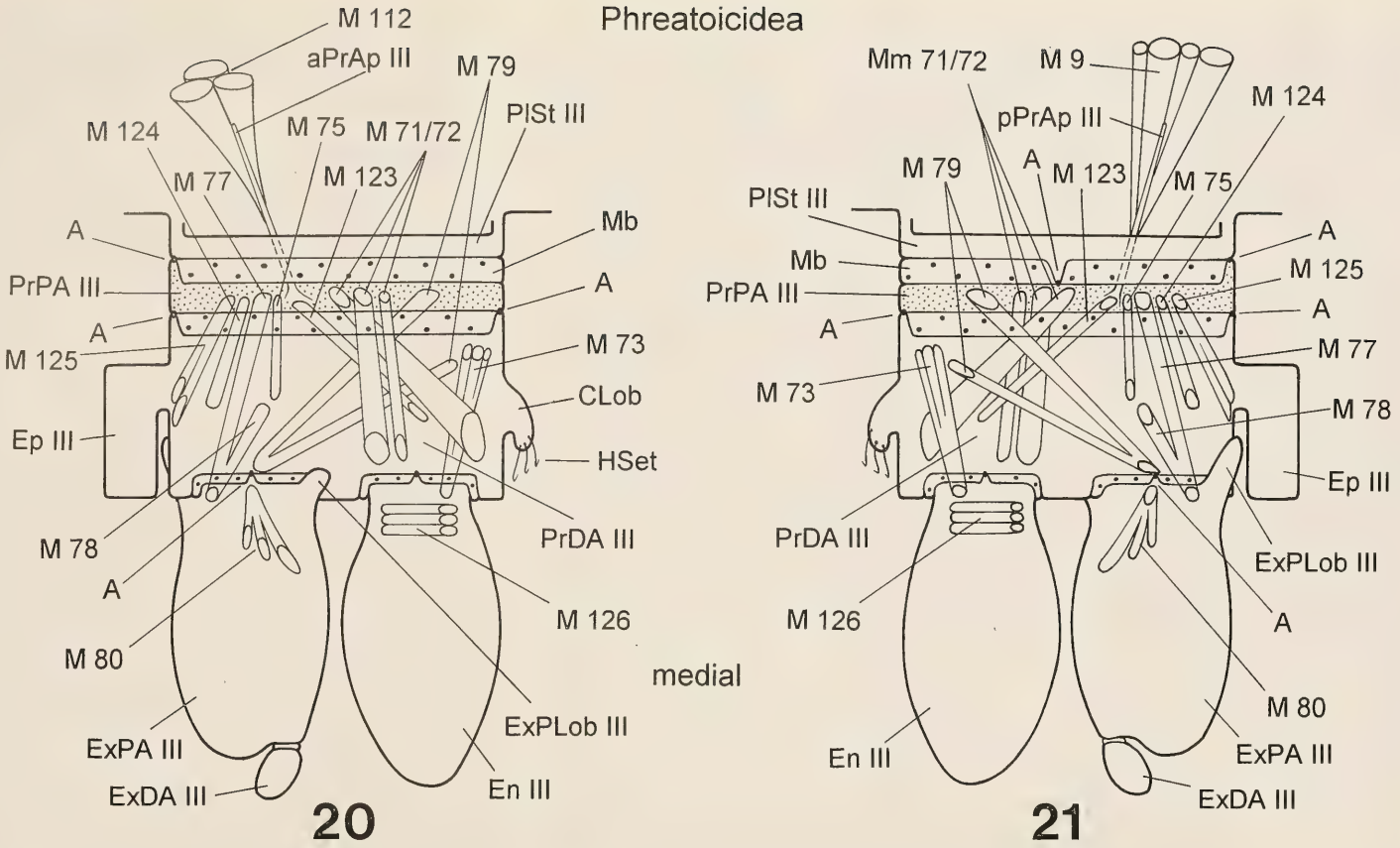
In the investigated species of *Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* the pleopod exopodites II–V are composed of two articles (figs. 12–13, 20–21). The distal joints are clearly movable. Between both segments a narrow articulation is developed. The pleopod exopodite I consists only of a single article, a distal one is missing (figs. 4–5).

The distal exopodite articles II–V in most phreatoicidean species (e.g. *Metaphreatoicus, Phreatoicopsis, Mesamphisopus*) are small and located distally at the proxi-

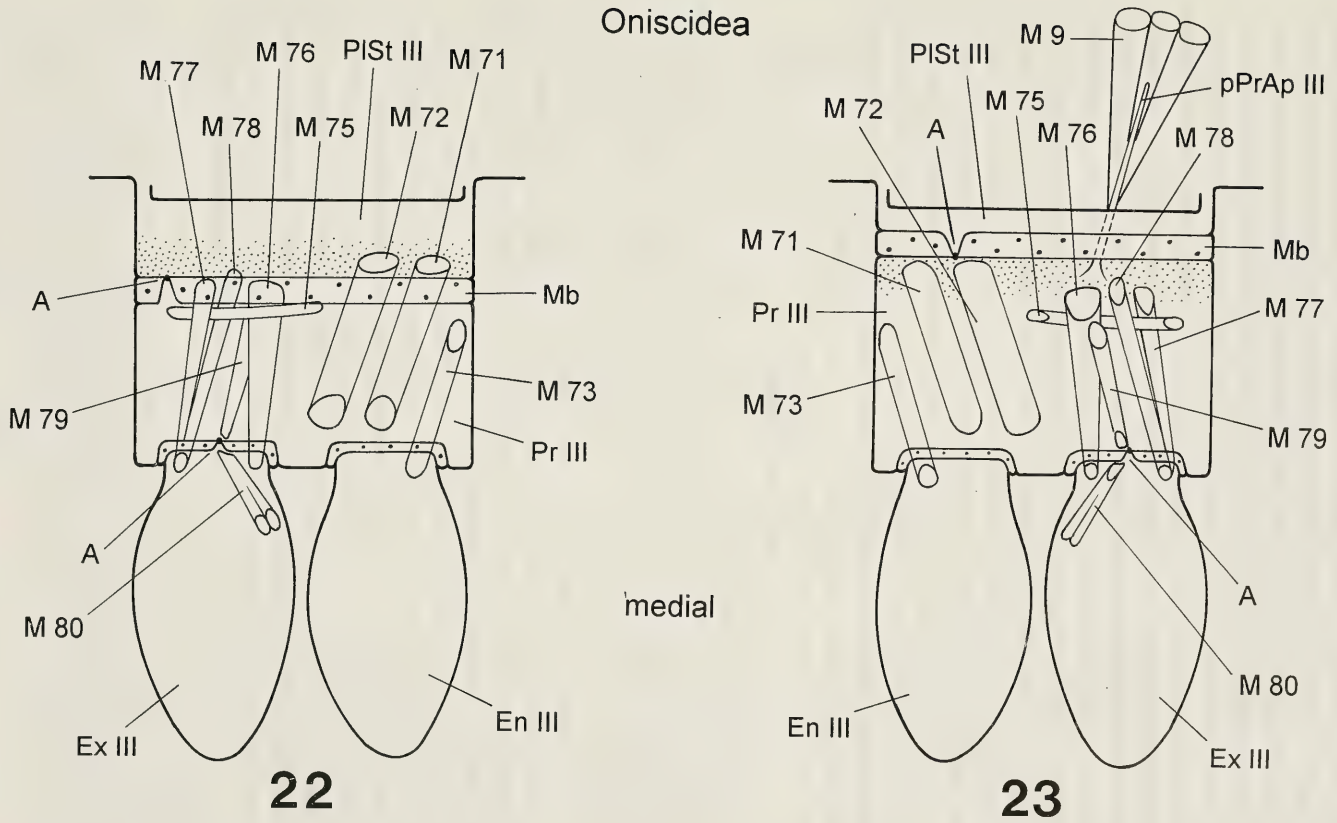
mal exopodite articles. *Nichollsia kashiensis,* however, has long distal articles inserting at the middle or proximal region of the medial walls of the proximal exopodite articles (cf. CHOPRA & TIWARI 1950: pl. 20, figs. 2–5).
Also in other isopod groups exopodites occur which are composed of two parts (e.g. Asellota, Cirolanidae, Aegidae, Sphaeromatidae, Valvifera, cf. GRUNER 1965–1966). However, WÄGELE (1989: 15) noticed that non-phreatoicidean isopods with two-jointed pleopod exopodites only have retained suture lines between both exopodite parts instead of an articular membrane wherefore the articles cannot be moved against each other. WÄGELE (1989: 232) explains this feature as apomorphous in relation to the isopodan and phreatoicidean groundpattern. In contrast, BRUSCA & WILSON (1991: 177) reported true biarticulated pleopod exopodites which are also present in basal asellotan groups like Aselloidea and Stenetrioidea.
WILSON & PONDER (1992: 295) assess the narrow articulation between the proximal and distal exopodite segments as an autapomorphous character state of the Phreatoicidea. In the incertae sedis-group *Tainisopus* and in the Asellota pleopodal exopodites occur which have broad articulation areas. In the Oniscidea the pleopod exopodites always are composed of one joint respectively (ERHARD 1995: 72) which might be an apomorphous character state in respect to the condition in the Phreatoicidea, Asellota and *Tainisopus.*

– Proximal lobes of the pleopod exopodites
In *Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Mesamphisopus* and less developed in *Nichollsia* the proximal exopodite articles of the pleopods II–V have medioproximal and lateroproximal lobes (figs. 12–13, 20–21). In *Phreatoicopsis terricola* corresponding lobes occur in the pleopod exopodites I–V. Following WILSON & KEABLE (in press), at least lateral exopodite enlargements are present in *Hyperoedesipus plumosus* and *Phreatoicoides gracilis* too. In the oniscidean groundpattern comparable lobes are not present (cf. ERHARD 1995, 1996, 1997).

– Lateral pleopod epipodites
In *Crenoicus* (WILSON & HO 1996) as well as in the investigated genera *Metaphreatoicus, Colubotelson, Onchotelson, Paramphisopus, Phreatoicopsis and Mesamphisopus* large lateral epipodites are present on the pleopod protopodites III–V. This character state might be a common feature of the Phreatoicidea. However, according to NICHOLLS (1943: 108), the phreatoicidean species *Eophreatoicus kershawi* retained lateral epipodites additionally on the pleopods II. Also in *Phreatoicopsis terricola* small lateral epipodites of the pleopods I and II could be shown. However, in *Hyperoedesipus, Phreatoicoides* (NICHOLLS 1943) and *Nichollsia* lateral epipodites of all pleopods are missing which might represent a secondary loss, possibly evolved during the invasion of hypogean habitats or surface-burrows. In the oniscidean groundpattern well-developed pleopod epipodites occur on the pleopods I and II but are missing on the pleopods III–V (figs. 6–7, 14–15, 22–23; cf. ERHARD 1995: 72). This pattern of characters indicates the presence of lateral epipodites at all five pleopod protopodites within the isopodan and phreatoicidean groundpatterns (figs. 4–5, 12–13, 20–21). Therefore, reductions of lateral epipodites on the pleopods I–V might represent apomorphous character states in respect to the isopodan groundpattern.



Figs. 20–21. Diagrams of the skeleton and musculature of the pleopods III within the groundpattern of the Phreatoicidea. Pleopodal rami projected onto the same level. Areas of the proximal protopodite articles indicated by *compact dotting*, membranes by *bold single dots*. – 20. Anterior view; – 21. posterior view.



Figs. 22–23. Diagrams of the skeleton and musculature of the pleopods III within the groundpattern of the Oniscidea. Pleopodal rami projected onto the same level. Areas of the proximal protopodite articles indicated by *compact dotting*, membranes by *bold single dots*. – 22. Anterior view; – 23. posterior view.

– Coupling lobes, setae and hooks

The presence of coupling setae or coupling hooks for the synchronization of the pleopodal blows represents a common feature within the Isopoda and other peracaridan taxa (NICHOLLS 1943: 21, WÄGELE 1989: 16). In *Mesamphisopus capensis* medial lobes of the distal articles of the pleopod protopodites I–V occur which are equipped with hooked setae. The first pleopod protopodite of *Paramphisopus palustris* has a small medial lobe covered with hooked setae, the protopodites of the pleopods II–V bear conspicuous lobes with long spines and few hooked setae. In *Colubotelson joyneri, Onchotelson brevicaudatus* and *Nichollsia kashiensis* the distal pleopod protopodite joints I–V and the protopodites II–V in *Metaphreatoicus australis* have medial lobes with few distally feathered setae (figs. 10, 18). The pleopod protopodites I of *Phreatoicopsis terricola* have medial nose-like lobes with hooked setae and the pleopod protopodites II-V possess finger-like coupling hooks at their medial wall.

According to NICHOLLS (1943: 21), the coupling hooks of phreatoicids might have developed from coupling lobes which, presumably, represent a groundpattern character of the Phreatoicidea (figs. 4–5, 12–13, 20–21). In the Oniscidea corresponding structures are missing (figs. 6–7, 14–15, 22–23) which might represent an apomorphous character state (cf. ERHARD 1995, 1996, 1997).

4.4.2. Musculature

– Pass of the intrinsic pleopod promotors

The muscles M 48, Mm 58/59 and Mm 71/72 of *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* work as intrinsic pleopod promotors stretched between the proximal and distal articles of the pleopod protopodites I–III (figs. 4–5, 12–13, 20–21). They are attached on the anterior walls of the proximal protopodite joints and are transmissing the power of the extrinsic pleopod promotors M 111, M 5 and M 112 to the distal protopodite articles. In contrast, M 48, Mm 58/59 and Mm 71/72 in the Oniscidea take their origins at the anterior parts of the pleon sternites I–III (figs. 6–7, 14–15, 22–23) because the anterior parts of the proximal protopodite articles obviously fused to the sternites (cf. chapt. 4.4.1.). This assumption implies an apomorphous character state of the Oniscidea in respect to the phreatoicidean condition.

The intrinsic pleopod promotors M 48 (pleopod I), Mm 58/59 (pleopod II) and Mm 71/72 (pleopod III) of the investigated phreatoicidean species are composed of 2–4 main units which often are crossing each other along its pass to the distal protopodite regions. The homologous muscles in the Oniscidea are formed by 1–2 units respectively. As far as they are formed by two units, they are always running side by side.

– Interarticular protopodite muscles Mm 51/115, 64/119/120, 75/124/125

The protopodite muscles Mm 51, 115 (pleopods I), Mm 64, 119, 120 (pleopods II) and Mm 75, 124, 125 (pleopods III) of the investigated phreatoicids *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* are interposing between the proximal and the distal protopodite articles (figs. 4–5, 12–13, 20–21). In the oniscid *Oniscus asellus* a small muscle bundle M 51 occurs in the pleopod protopodite I (ERHARD 1995: 35) which might be homologous to M 51 of the Phreatoicidea on account of their corresponding passes.

Undoubtedly, in phreatoicidean species the serial homologa to M 51 within the pleopods II and III are the muscles M 64 and M 75. Presumably, they are homologous to the oniscidean muscles M 64 and M 75 despite of slight differences concerning their passes (figs. 4–7, 12–15, 20–23; cf. ERHARD 1995, 1996, 1997).
In contrast, homologa to the muscles M 115 (pleopods I), Mm 119 and 120 (pleopods II) as well as Mm 124 and 125 (pleopods III) of the phreatoicidean species could not be identified within the oniscidean species investigated so far (cf. ERHARD 1995, 1996, 1997). Probably, comparable muscles in the Oniscidea have been reduced because free proximal protopodite articles between the sternites and the distal protopodite regions are not present in terrestrial isopods. Only in the basal *Ligia oceanica* the muscle M 69 which is described as locomotor of the lateral pleopod epipodite II (ERHARD 1995: 47) shows a comparable run with M 120 in the pleopods II of *Metaphreatoicus.* However, the point of origin of M 69 in *Ligia* is situated on the anterior wall of protopodite II and not on the posterior wall as it is the case with M 120 of *Metaphreatoicus.* Therefore, a homologization seems to be difficult.
The occurrence of two pleopod protopodite joints in the Phreatoicidea was interpreted above (chapt. 4.4.1.: "Protopodite joints") as an ancestral condition among isopods. Simultaneously, it has to be assumed that the oniscidean protopodites, formed by only one joint respectively, originate by fusion of two (or three) joints. The lack of the interarticular protopodite muscles Mm 115, 119–120 and 124–125 in the Oniscidea then might be explained by secondary loss after the fusion of the protopodite joints during evolution because the muscles could not longer function as locomotors between immovable articles. This scenario implies that the presence of the interarticular muscles in the Phreatoicidea might represent a plesiomorphous state in relation to the apomorphous condition in the Oniscidea.

– Interarticular protopodite muscles Mm 116, 122 and 123

The muscles could be shown in the pleopods I (M 116), II (M 122) and III (M 123) of *Metaphreatoicus australis* and *Onchotelson brevicaudatus,* M 122 additionally could be determined in *Phreatoicopsis terricola* and M 116 in *Paramphisopus palustris* (figs. 4–5, 12–13, 20–21). Serial homologous muscles, presumably, may occur also in the pleopods IV and V of the same species. In the Oniscidea muscles with a comparable run are missing (cf. ERHARD 1995, 1996, 1997). M 116, M 122 and M 123 of *Metaphreatoicus, Onchotelson, Paramphisopus* and *Phreatoicopsis* are interarticular locomotors interposing between proximal and distal protopodite articles. A secondary loss of their homologa within the Oniscidea which possess only one protopodite article, therefore, would be obvious (see also preceding paragraph).
However, in *Ligia oceanica* a muscle M 68 occurs within the pleopod II which is stretched between the posterior and anterior protopodite wall (cf. ERHARD 1995: 49). This is also the case with M 122 inside the pleopod protopodite II of *Metaphreatoicus, Onchotelson* and *Phreatoicopsis,* but in contrast to M 68 of *Ligia* the points of origin and insertion seem to be exchanged. Thus, a homologization appears to be difficult.

– Medial exopodite locomotors

Within the pleopod I of the oniscid *Ligia oceanica* two medial exopodite locomotors M 53 and M 56 occur (figs. 6–7; cf. ERHARD 1995: 38). On account of their

comparable pass both muscles can be homologized with the two medial exopodite I-locomotors M 53 and M 56 of *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* (figs. 4–5; cf. chapt. 4.1.1.2.). In the pleopods I of the oniscidean taxa Mesoniscidae, Synocheta and Crinocheta only one medial exopodite locomotor M 50 occurs (ERHARD 1995, 1996, 1997) which, presumably, is homologous to M 53 of *Ligia* and of the phreatoicidean species. This might be indicated by the extreme medial point of insertion of the corresponding muscles.

Within the pleopods II of *Metaphreatoicus, Onchotelson, Paramphisopus* and *Phreatoicopsis* the medial exopodite locomotors are composed of three bundles (single branch of M 63 and two bundles of M 118; figs. 12–13). There is no doubt that the medial branch M 63 is serially homologous to M 53 within the pleopods I of *Metaphreatoicus* because of their completely corresponding appearance. In contrast, inside the second pleopods of *Metaphreatoicus, Onchotelson, Paramphisopus* and *Phreatoicopsis* the muscle M 118, serial homologon to M 56 (pleopods I), obviously consists of two branches (only one branch in *Mesamphisopus capensis*). In *Metaphreatoicus australis* and *Paramphisopus palustris* one bundle originates on the proximal and the other on the distal protopodite II-article while in *Onchotelson brevicaudatus* both bundles take their origin on the proximal protopodite II-article. Within the pleopods II of oniscidean species only one medial exopodite locomotor M 63 is developed (figs. 14–15; cf. ERHARD 1995, 1996, 1997). In *Mesamphisopus capensis* M 63 and a single branch of M 118 is present, the latter takes its origin on the proximal protopodite joint.

In contrast to the pleopods I and II, the pleopod III of *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus* has retained only the medial exopodite locomotor M 79 (figs. 20–21) which is serially homologous to M 56 (pleopod I) and M 118 (pleopod II) on account of their corresponding positions. The pleopods III obviously have lost the other medial exopodite locomotor M 76 which would be serially homologous to M 53 (pleopod I) and M 63 (pleopod II). However, in *Ligia oceanica* both medial exopodite locomotors M 76 und M 79 within the pleopod III are retained (figs. 22–23; cf. ERHARD 1995: 61). In contrast to the phreatoicidean species M 79 of *Ligia* is composed of one bundle which originates on the posterior wall of the protopodite III-article whereas in *Metaphreatoicus, Onchotelson, Paramphisopus* and *Mesamphisopus* two bundles are present and the points of origin are located at the proximal as well as the distal protopodite III-article. Within the pleopods III of the Oniscidea-Holoverticata (= Tylidae + Mesoniscidae + Synocheta + Crinocheta, cf. ERHARD 1998b) the muscle M 79 is missing (ERHARD 1995, 1996, 1997). Presumably, the latter character represents an autapomorphous state of the Oniscidea-Holoverticata in respect to the oniscidean groundpattern.

How to interprete the different character states of the phreatoicids and the oniscids? Concerning the medial exopodite locomotors M 53 and M 56 of the pleopods I the conditions of *Metaphreatoicus* and *Ligia* seem to be correspondent (figs. 4–7). While the pleopods II of the phreatoicids bear both medial exopodite locomotors M 63 and M 118, within the oniscidean groundpattern only M 63 is retained (figs. 12–15; cf. ERHARD 1995, 1996, 1997). The complete reduction of M 118 probably might represent an apomorphous character state of the Oniscidea. On the other hand, the Phreatoicidea seem to be apomorphous concerning

the complete reduction of M 76 inside the pleopods III while the Oniscidea-Ligiidae have preserved the plesiomorphous status with both medial exopodite locomotors M 76 and M 79 (figs. 20–23; comparable conditions occur also within the pleopods IV and V). Concerning the composition of M 79, presumably, *Metaphreatoicus, Onchotelson, Paramphisopus* and *Mesamphisopus* have retained the plesiomorphous character state with two bundles originating on the proximal and distal protopodite articles. *Ligia* and thus the oniscidean groundpattern show the apomorphous condition with only one branch which might be caused by the fusion of the different protopodite articles during evolution (cf. chapt. 4.4.1.: "Protopodite joints").

– Lateral exopodite locomotors (Mm 54/55, 65/66, 77/78)

In the Oniscidea lateral pleopod exopodite I-locomotors comparable to Mm 54 and 55 of *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* could only be shown until now in *Ligia oceanica* (figs. 4–7; cf. ERHARD 1995: 38). In the latter species M 55 takes its origin **posteriorly** on the protopodite I while M 54 originates on the **anterior** wall of the protopodite I. In contrast, in the phreatoicidean species both muscles take their origin on the same location, that is the **posterior** side of the distal article of protopodite I.

Within the pleopods II–V of *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus* the serial homologous muscle pairs also arise on the posterior protopodite wall but with one branch on the proximal and the other on the distal protopodite article. Inside the pleopods III–V of the basal oniscid *Ligia oceanica* the lateral exopodite locomotors Mm 77/78, 87/88, 95/96 also take their origin only on the posterior protopodite wall (figs. 12–15, 20–23; cf. ERHARD 1995: 61). On the other hand, the points of origin of the muscle pairs Mm 54/55 and Mm 65/66 in the pleopods I and II of *Ligia* and the muscles Mm 65/66, 77/78, 87/88, 95/96 within the pleopods II–V of the Oniscidea-Orthogonopoda (= Mesoniscidae + Synocheta + Crinocheta, cf. TABACARU & DANIELOPOL 1996) are located anteriorly and posteriorly. The polarity of this character has to be checked by future out- and ingroup comparisons.

The lateral exopodite locomotors in the pleopods II–V in the phreatoicids have their origin posteriorly on the proximal as well as on the distal protopodite article. Within the Oniscidea the protopodites are no more biarticulated (cf. chapt. 4.4.1.: "Protopodite joints") wherefore a phreatoicidean-like differentiation of the muscle origins does not occur. This feature has to be considered as an apomorphous state in respect to the phreatoicidean groundpattern.

– Pleopod exopodite locomotors Mm 57, 67 and 80

The pleopod exopodites I–III of *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* as well as the oniscid *Ligia oceanica* contain the muscles M 57, M 67 and M 80 (figs. 4–7, 12–15, 20–23; cf. ERHARD 1995). In the Oniscidea-Orthogonopoda (= Mesoniscidae + Synocheta + Crinocheta) the muscle M 57 within the pleopod I is completely reduced. Additionally, the muscle M 80 within the pleopod III of the Oniscidea-Crinocheta is missing (ERHARD 1995). Comparable exopodite locomotors within all pleopods of *Tylos ponticus* (Oniscidea-Tylidae) are completely reduced (ERHARD 1995).

In the phreatoicidean species Mm 57, 67 and 80 originate on the posterior exopodite bases and are inserted on the anterior exopodite walls. This pattern also occurs in the retained muscles of the oniscid groups Mesoniscidae, Synocheta and Crinocheta and might be present in the phreatoicidean and oniscidean groundpattern. However, in *Ligia oceanica* the points of insertion of the muscles have changed to the posterior walls of the exopodites (ERHARD 1995). This feature might represent an apomorphous character state of *Ligia* in respect to the oniscidean groundpattern.
The muscles Mm 57, 67 and 80 are composed of three (*Metaphreatoicus, Onchotelson, Phreatoicopsis, Mesamphisopus*), two (*Nichollsia, Ligia, Titanethes, Actaecia*) or one bundle respectively (*Paramphisopus, Mesoniscus, Oniscus*) (cf. ERHARD 1995, 1996, 1997).

– Composition of the pleopod endopodite locomotors Mm 61, 73
In *Metaphreatoicus, Onchotelson, Paramphisopus, Mesamphisopus* and *Nichollsia* the serial homologous locomotors Mm 61 and 73 of the pleopod endopodites II and III are composed of two or three bundles while the homologous muscles of all oniscidean species investigated so far consist of single strands respectively (figs. 12–15, 20–23; cf. ERHARD 1995, 1996, 1997).

– Intrinsic endopodite muscles Mm 117, 121, 126
The pleopods I–III of *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus* bear one intrinsic endopodite muscle respectively (M 117, M 121, M 126; figs. 4–5, 12–13, 20–21). Serial homologa to these muscles also appear in the pleopods IV and V. In *Nichollsia* only the muscle M 121 within the male pleopod endopodite II could be shown with certainty. Within the Oniscidea intrinsic endopodite muscles comparable to M 117, 121 and 126 of the Phreatoicidea could not be found (figs. 6–7, 14–15, 22–23; cf. ERHARD 1995, 1996, 1997). An exception represents M 49 within the male pleopod endopodites I in the Oniscidea-Crinocheta but as already discussed (chapt. 4.1.2.: "M 117") this feature might be an autapomorphous character state of the Crinocheta.

5. Uropods

5.1. *Metaphreatoicus australis* (figs. 24–27)

5.1.1. Skeleton

The styliform uropods of *Metaphreatoicus australis* are inserted on anterior lateroventral extensions of the pleotelson (figs. 24–26: vPtExt) which are formed by ventrally directed lateral lengthenings of the pleotelsonic tergite and sternite. Together with the strong downward developed epimera of the pleon segments I–V these lateral sacs at both pleotelson sides, which are flattened laterally, are forming a voluminous chamber wherein the pleopods are located (fig. 30; cf. ERHARD 1998a: 7). The pleotelsonic extensions give origin to the ventrally positioned uropods what might be favourable for the special type of phreatoicidean locomotion. This is caused by strong thrusts of the pleotelson and the uropods onto the substrate whereupon the isopod moves forwards (cf. NICHOLLS 1943: 57, GUPTA 1989: 12, ERHARD 1998a: 13).

Between the anterior lateroventral extension of the pleotelson and the uropod protopodite a dicondylic articulation is developed (figs. 24–25). The articular points are located medioventrally and laterodorsally at the basis of the protopodite wherefore the latter is movable in dorsomedial and ventrolateral direction. The protopodite levators Mm 97–98 are inserted on a long dorsomedial apophysis whereas the protopodite depressors Mm 99–100 terminate at a long lateroventral apophysis.

As it is the case of the lateroventral pleotelsonic extensions also the uropod protopodites are flattened laterally thus partly forming the terminal end of the lateral wall of the pleopodal chamber (fig. 30; ERHARD 1998a: fig. 2). The uropod protopodites have two longitudinal dorsal ridges which are equipped with numerous strong spines. Near the ventral bases of the uropodal rami two strong spines are inserted on the distal end of the uropod protopodite which have hand-like (spinose) tips (figs. 26–27).

The uropod exo- and endopodite are about equal in size. Both rami are inserted distally on the uropod protopodite. At their distal ends separate joint-like tips are developed (fig. 26). The uropod exopodite of *Metaphreatoicus australis* is remarkable for the presence of a conspicuous dorsolateral spine at the middle of its length (fig. 25). Between the uropod protopodite and the exo- and endopodites dicondylic articulations are developed. The articular points are located laterally and medially at the bases of the uropodal rami, wherefore, they are movable in dorsal and ventral directions (this articular arrangement is also present in further phreatoicids like *Phreatoicopsis*). The uropod exopodite basis has developed ventral and dorsal apophyses which serve as attachment points for the exopodite depressor M 101 and the levator M 102 (fig. 25). At the endopodite basis only a ventral apophysis is present whereon the endopodite depressor M 103 is inserted (fig. 24). As it is the case in all eumalacostracan species (cf. ERHARD 1995: 95) an endopodite levator does not exist in *Metaphreatoicus*, the back movement of the endopodite in dorsal direction occurs passively.

5.1.2. Musculature

M 97: Moves the uropod protopodite in dorsomedial direction. The strong fan-shaped muscle arises on the lateral wall of the anterior lateroventral pleotelsonic extension (= lengthening of the pleotelsonic tergite) and is inserted on the dorsomedial apophysis of the uropod protopodite basis. Composed of about 6–7 bundles.

M 98: Moves the uropod protopodite in dorsomedial direction. Arises on the medial wall of the lateroventral pleotelsonic extension (= lengthening of the pleotelsonic sternite) and is inserted on the dorsomedial apophysis and on the medial basis of the uropod protopodite. Composed of about three bundles.

M 99: Moves the uropod protopodite in ventrolateral direction. The strong fan-shaped muscle arises on the lateral wall of the lateroventral pleotelsonic extension and is inserted on the ventrolateral apophysis of the uropod protopodite basis. Composed of about 6–7 bundles.

M 100: Moves the uropod protopodite in ventrolateral direction. Arises on the medial wall of the lateroventral pleotelsonic extension and is inserted on the ventrolateral apophysis of the uropod protopodite basis. Composed of about four small bundles.

M 101: Depressor of the uropod exopodite. Arises with two bundles on the laterodorsal basis of the uropod protopodite and with three bundles on the medioven-

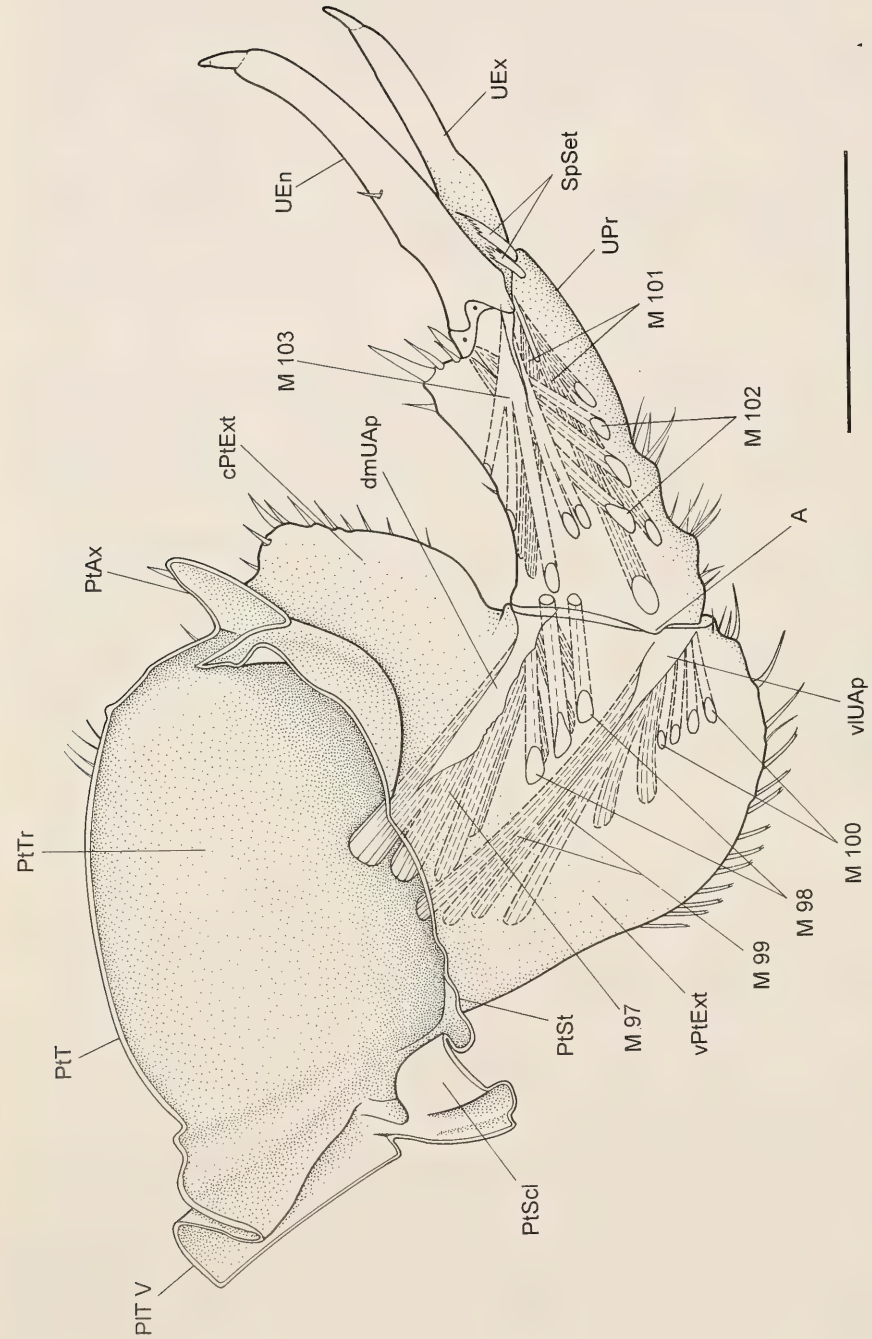


Fig. 24. *Metaphreatoicus australis*, ♂, median longitudinal section through the pleotelson in medial view showing the skeleton and musculature of the right uropod. – Scale: 1 mm.

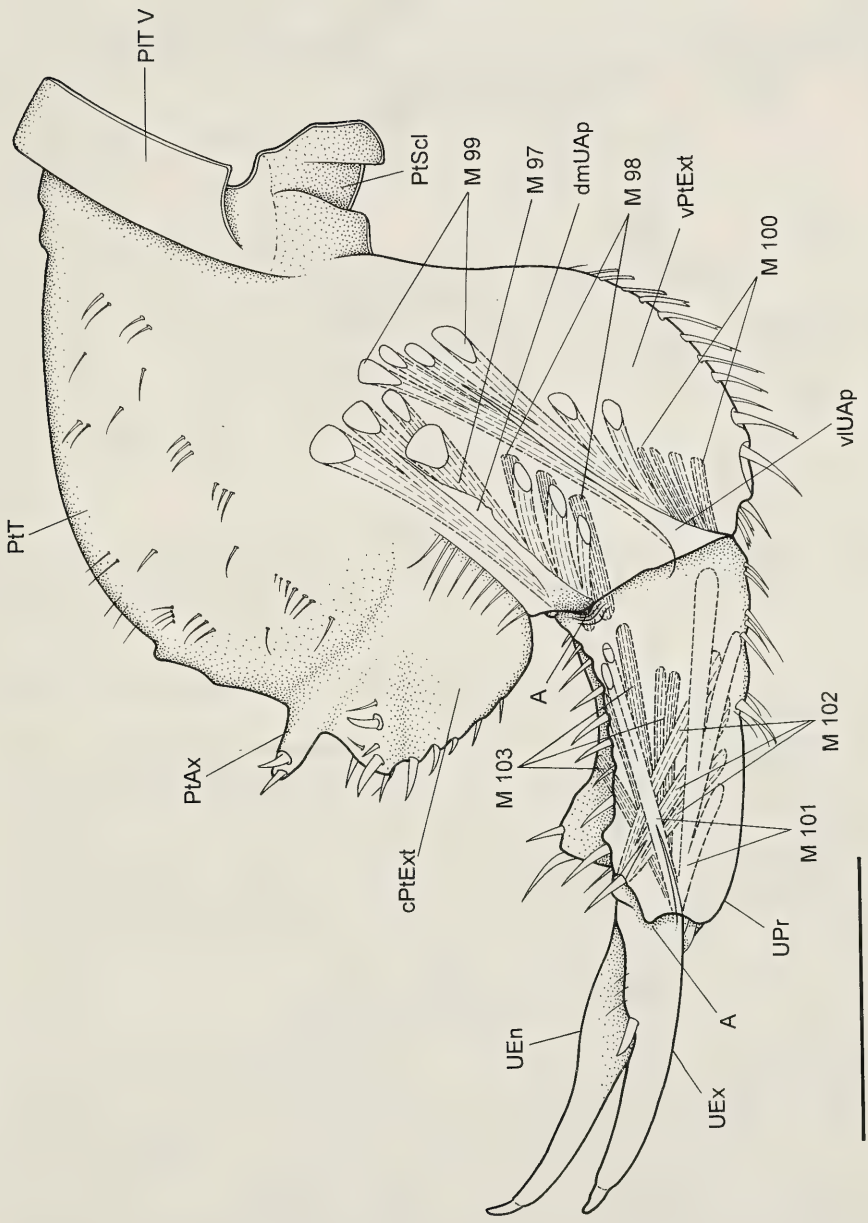
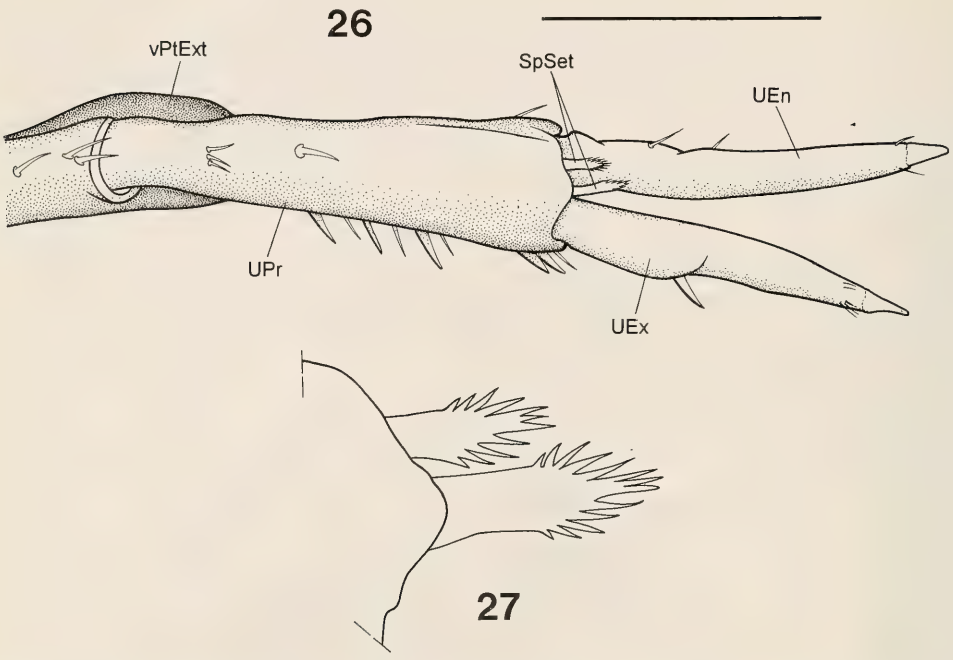


Fig. 25. *Metaphreatoicus australis*, ♂, right side of pleotelson in lateral view showing the skeleton and musculature of the right uropod. – Scale: 1 mm.



Figs. 26–27. *Metaphreatoicus australis*, ♂, right uropod. – 26. Ventral view. Scale: 1 mm. – 27. Ventrally positioned spinose setae on the distal end of the uropod protopodite.

tral wall of the protopodite. The muscle is inserted on the ventral apophysis of the uropod exopodite basis.

M 102: Levator of the uropod exopodite. Arises with about three bundles on the medioventral wall of the uropod protopodite and is inserted on the dorsal apophysis of the uropod exopodite basis. M 102 is located between M 101 and M 103.

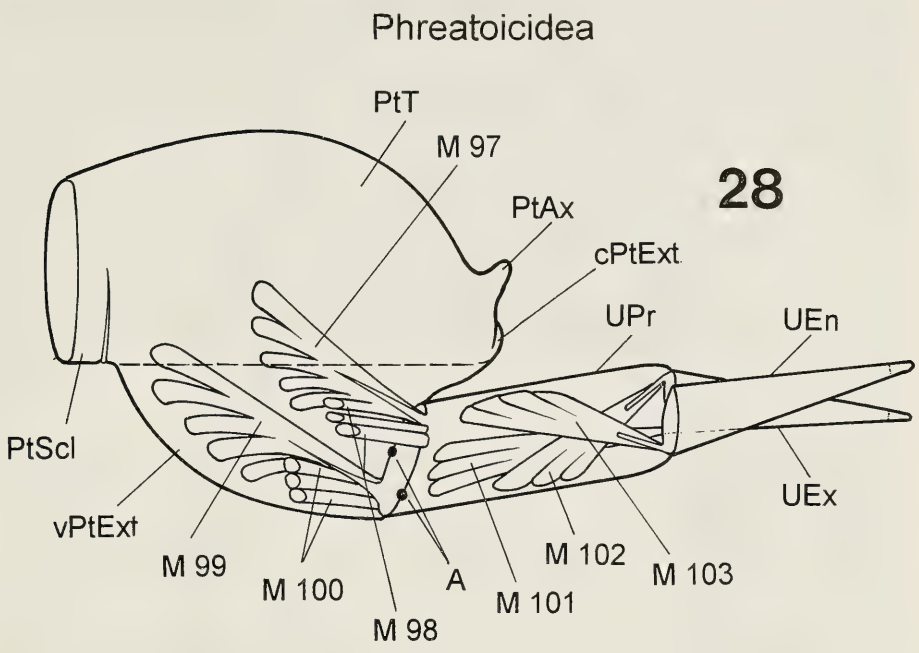
M 103: Depressor of the uropod endopodite. Arises with about three bundles on the medial basis of the uropod protopodite and with two bundles on the dorsal protopodite wall. The muscle is inserted on the ventral apophysis of the uropod endopodite basis.

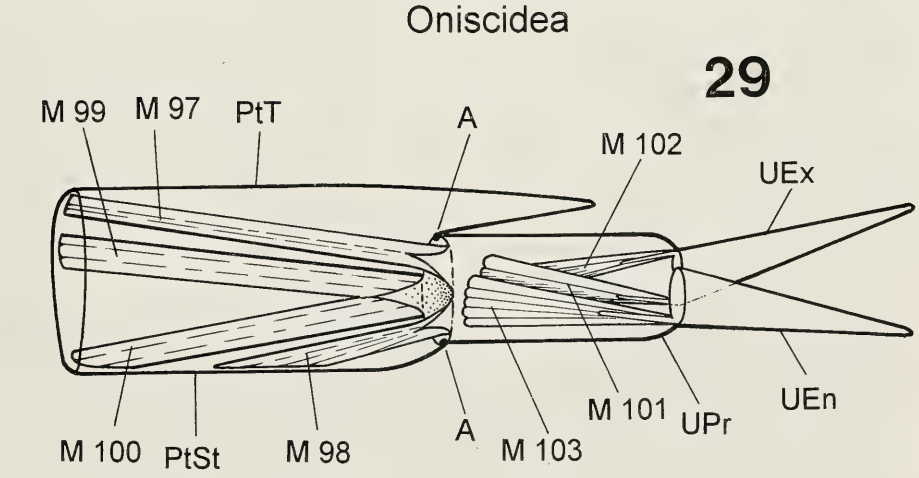
5.2. Comparison (figs. 28–30)

– Insertion area of the uropods

In view of the fact that the uropods arise from the sixth pleonite in malacostracans, which is fused with the telson in isopods, the anteriolateral position of the uropods at the pleotelson in most phreatoicidean species (e.g. *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus)* is assumed to be a plesiomorphous character state in respect to the isopodan groundpattern (cf. WÄGELE 1994: 93). The subterminal insertion present for example in the Oniscidea and Asellota, probably, might be an apomorphous condition (cf. WÄGELE 1994: 93).

A secondary feature in respect to the phreatoicidean groundpattern might also be the subterminal insertion of the uropods in adult specimens of the genus *Nicholl-*





Figs. 28–29. Diagrams of the skeleton and musculature of the uropods within the Isopoda in medial view. – 28. Groundpattern Phreatoicidea; – 29. groundpattern Oniscidea.

sia (cf. Choppa & Tiwari 1950: pl. 20, fig. 2). The anterior insertion of the uropods, probably, was given up after the evolutionary loss of the pleopodal chamber and the reduction of the anterior lateroventral pleotelsonic extensions (figs. 24–26, 30: vPtExt) which serve as area of insertion for the uropods in surface living phreatoicideans. This reduction might be caused by the change of habitats from surface to ground waters presumably performed by the ancestors of *Nichollsia.*

However, the uropods in newly hatched young specimens of *Nichollsia kashiensis* have more posteriorly situated points of insertion and the pleotelson has an intimated lateroventral extension whereon the uropods are located (cf. Gupta 1989: 34, fig. 8). This ontogenic character state resembles the situation present in surface living phreatoicideans. It might underline that also the ancestors of *Nichollsia* have had lateroventral pleotelsonic extensions partly forming a pleopodal chamber.

– Pleopodal chamber

The anterior lateroventral pleotelsonic extensions (figs. 24–25: vPtExt) present e.g. in *Crenoicus* (cf. Wilson & Ho 1996), *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis* or *Mesamphisopus* serve like the enlarged pleonal epimera and the laterally flattened uropod protopodites as lateral walls of the pleopodal chamber (figs. 24–25, 30; cf. Erhard 1998a: 13). Furthermore, they function as exposed insertion regions for the ventral positioned uropods which are used as anklebones during the special type of locomotion of disturbed animals by powerful thrusts of the pleotelson onto the substrate. The lateroventral pleotelsonic extensions as well as the whole pleopodal chamber seem to be unique among isopods and peracarids and, therefore, might represent an apomorphous groundpattern character of the Phreatoicidea (cf. Erhard 1998a: 7).

Solely in the stygobiontic phreatoicid genera *Nichollsia, Hyperoedesipus, Phreatoicoides (P. longicollis, P. wadhami)* and *Hypsimetopus* the downward development of the pleonal epimera and the formation of a ventral pleopodal chamber is missing. According to Knott (1986), Wägele (1990), Erhard (1998a: 7) and Wilson & Keable (in press) the above mentioned ground water forms and burrowers might be derived from surface-cryptic phreatoicids[1]) and the reduction of the pleopodal chamber, presumably, represents an adaptation to the life in interstitial habitats and burrows (cf. chapt. 6.).

As already reported by Erhard (1998a: 9) the superficial similarity of "ventral chambers" in amphipodan and phreatoicidean species in all probability might be caused by convergent evolution. Concerning the external pleon anatomy, well-founded synapomorphies of the Amphipoda and Isopoda (Phreatoicidea) cannot be shown. The presence of lateroventral pleotelsonic extensions as well as a vaulted pleotelson is limited to the Phreatoicidea, while in the Amphipoda (Gammaridea) a different construction of the pleonite VI and the telson occurs. The amphipodan ventral channel is formed by epimera of the thoracomeres and the pleon segments I–III while, in contrast, in the Phreatoicidea chiefly the pleomeres III–V and the voluminous pleotelson are involved in forming the pleopodal chamber.

[1]) Ecotypes according to Wilson & Keable (in press).

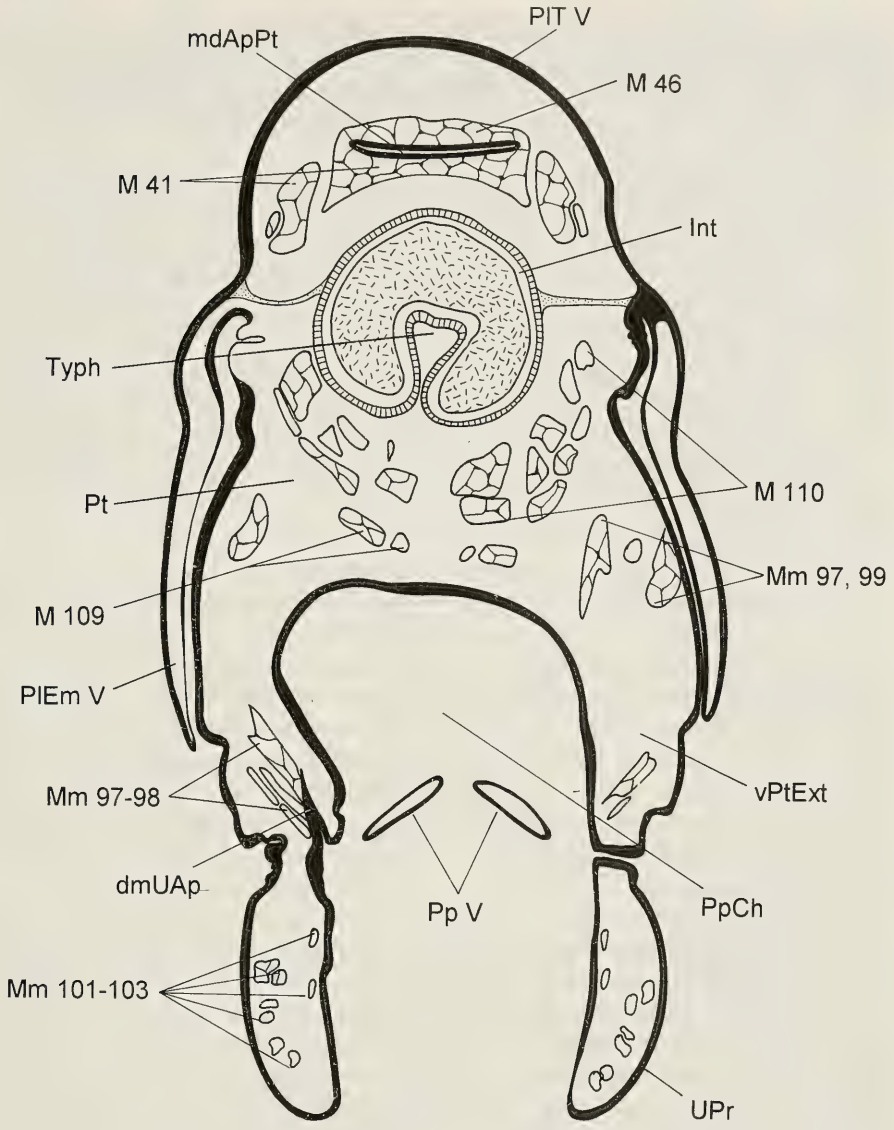


Fig. 30. *Metaphreatoicus australis*, ♂, cross-section through the posteriodorsal region of the pleonite V and the anterioventral region of the pleotelson showing the pleopodal chamber *(PpCh)*. For the detailed description of Mm 41, 46 and 109–110 compare ERHARD (1998a).

The apomorphous character complex of the pleopodal chamber in phreatoicideans might comprise not only the features of enlarged pleon epimera, lateroventral pleotelsonic extensions and laterally flattened uropod protopodites. With all probability also the dorsally curved pleotelsonic apex and the adjacent regions of the caudal pleotelsonic margin (figs. 24–25: cPtExt), which cover the terminal opening of the ventral chamber in most surface-living species, are included in the

functional complex (cf. ERHARD 1998a: 9). Therefore, the reduction of a dorsally curved pleotelsonic apex in the stygobiontic forms *Nichollsia, Hyperoedesipus, Phreatoicoides* and *Hypsimetopus* does not surprise because in those groups also other components of the pleopodal chamber like enlarged pleon epimera are reduced.

On the other hand, in species whose pleopodal chamber is formed in a perfect manner as in *Onchotelson brevicaudatus* (cf. ERHARD 1998a: 9), *Uramphisopus pearsoni* (cf. NICHOLLS 1943) and *Mesacanthotelson tasmaniae* the pleotelsonic apex is developed very conspicuously and is curved dorsally. Following NICHOLLS (1943, 1944) these three species are living inside the muddy floor of the Great Lake in Tasmania. This, probably, might indicate that the pleopodal chamber originally could have a protective action against pollution of the respiratory pleopods by muddy water. In this connection, the long dorsally curved apex and the adjacent pleotelsonic regions could serve as guiding structures for a controlled instream of clear and oxygenous water. Observations on living phreatoicids would, presumably, show functional aspects of the pleopodal chamber and could, therefore, test the above mentioned hypothesis.

– Arrangement of the uropodal muscles and articular points

A comparison of the uropodal muscles of the Oniscidea (cf. ERHARD 1995, 1996, 1997) and the isopod groups Phreatoicidea, Anthuridea, Gnathiidae and "Flabellifera" (cf. WÄGELE 1981, 1994) as well as the eumalacostracan taxa Amphipoda (cf. BÖRNER 1921), Decapoda (cf. SCHMIDT 1915, BERKELEY 1928, PATERSON 1968, WÄGELE 1994), Euphausiacea (cf. WÄGELE 1994) and Syncarida (cf. DANIEL 1932) was drawn by ERHARD (1995: 95). Following this, the pattern of the different uropodal muscles is generally identical within the mentioned isopodan and malacostracan taxa. Obviously, the uropod musculature present in the extant eumalacostracan species might be a conservative character complex retained over hundred of million years.

Thus, all oniscidean and phreatoicidean uropodal muscles (Mm 97–103) can be easily homologized. All uropodal muscle units, which are present in the Oniscidea, occur in the Phreatoicidea as well. WÄGELE (1994: 93), however, describes only two distinct uropodal protopodite locomotors ("M. IV" and "M. VI" = M 97 and M 99) of *Mesamphisopus capensis* but own observations on the same species could determine the complete set of four protopodite locomotors Mm 97–100 with clearly different points of attachment. These result are exactly in conformity with the situations present in *Metaphreatoicus* (cf. chapt. 5.1.2.), *Onchotelson, Paramphisopus, Phreatoicopsis* and *Nichollsia* as well as with the oniscidean groundpattern (ERHARD 1995: 95).

In spite of the unambiguous homologization of the uropodal muscles, differences between Phreatoicidea and Oniscidea occur which concern the spatial arrangement of the musculature. Within the oniscidean groundpattern the uropod protopodites insert subterminally on the pleotelson and are movable in lateral and medial direction on account of a dorsoventral articular axis. The apophyses of the protopodite locomotors are situated laterally and medially to the articular axis. The protopodite locomotors of the Oniscidea take their origin at the pleotelsonic tergite and sternite side by side and near the front margin of the pleotelson (fig. 29; cf. ERHARD 1995: 95).

In the investigated phreatoicids *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus* the uropod protopodites are inserted on the lateroventral pleotelsonic extensions. These extensions serve as walls forming caudolateral parts of the ventral chamber wherein the pleopods are situated. They are formed by lateral lengthenings of the pleotelsonic tergite and sternite. During the evolution of the extensions the origins of the protopodite muscles Mm 97–100 have been shifted ventrally and are now attached on the lateral and medial walls of the pleotelsonic extensions (figs. 24–25, 28).

In contrast to the oniscidean situation, the uropod protopodites of *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* are movable in dorsomedial and ventrolateral directions, probably, to support the locomotory thrusts of the pleotelson onto the substrate. In consequence, the articular points between pleotelson and uropod protopodite are forming an axis which passes from ventromedial to lateral and the protopodite apophyses are situated ventrolaterally and dorsomedially. The protopodite muscles of those phreatoicids with lateroventral pleotelsonic extensions (e.g. *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus)* are positioned one behind the other ("serially" following WÄGELE 1994: 93) and they originate for the most part far away from the pleotelson front margin (fig. 28).

Presumably, these muscular and articular arrangements are corresponding to the formation of the pleopodal chamber. The anterior lateroventral extensions of the pleotelson are assumed to be an apomorphous character of the Phreatoicidea (see preceding paragraph and ERHARD 1998a: 7). Therefore, the spatial muscular and articular arrangement of the phreatoicidean uropods also might partly represent derived conditions in respect to the situation in oniscids and other isopod groups and not inevitably a plesiomorphous character state as supposed by WÄGELE (1994: 93). However, further out- and ingroup comparisons are necessary to make clear statements.

In *Nichollsia kashiensis* a pleonal chamber and anterior lateroventral pleotelsonic extensions do not exist. The uropod protopodite locomotors Mm 97–100 are located laterally within the main pleotelsonic lumen as it is for example also the situation in the Oniscidea. The very strong muscles Mm 97–98 are formed by a large number of bundles whereas Mm 99–100 are less developed. The latter are positoned laterally to Mm 97–98. The different muscle arrangement, compared with the situation in surface living phreatoicids, and generally the worm-like appearance of *Nichollsia* are considered here as a result of secondary reduction of the pleonal chamber caused by the invasion of ground water habitats (cf. chapt. 6.).

– General shape of the uropods

All species of the Phreatoicidea have styliform uropods. This is also the case in the Asellota (incl. Microcerberidae), Oniscidea, *Tainisopus,* Bopyridae and the peracaridan outgroups Amphipoda, Cumacea, Mictacea and Tanaidacea. In contrast, broad and flat uropods forming a tail fan are present in the Gnathiidae, Anthuridea and in flabelliferan groups as well as in the peracaridan outgroups Mysida, Lophogastrida and Spelaeogriphacea (cf. GRUNER 1993). The uropods of the Calabozoida and the Valvifera are strongly derived wherefore a clear categorization seems to be difficult.

Controversal discussions on the polarity assessment concerning the character "shape of the uropods" are presented by WÄGELE (1981, 1989, 1994), SCHMALFUSS (1989), BRUSCA & WILSON (1991) and WILSON (1996).

– Shape of the uropod protopodites

The uropod protopodites of surface living phreatoicids (e.g. *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus*) are flattened laterally and contribute to the formation of the pleopodal chamber (figs. 24–26, 30). This chamber as well as the flattened shape of the uropod protopodite are assumed to be autapomorphous character states of the Phreatoicidea (see previous paragraphs).

The uropod protopodites of *Nichollsia kashiensis* are not flattened but show a circular cross-section. This appearance might be caused by the evolutionary loss of the pleopodal chamber in the ancestors of *Nichollsia* during the invasion of subterranean interstitial waters. In the oniscidean groundpattern the protopodites are flattened in the dorsoventral plane or show a sub-circular sectional view. A pleopodal chamber is also missing (cf. ERHARD 1995, 1996, 1997).

– Dorsal ridges of the uropod protopodites

In the investigated phreatoicidean genera *Metaphreatoicus, Colubotelson, Onchotelson, Mesacanthotelson, Paramphisopus, Phreatoicopsis, Mesamphisopus* and *Nichollsia* the dorsal walls of the uropod protopodites have medial and lateral longitudinal ridges which often are equipped with numerous strong setae (fig. 25). In the oniscidean species investigated so far (cf. ERHARD 1995, 1996, 1997) as well as in the tanaid *Apseudes* comparable ridges are missing.

– Distal spines of the uropod protopodite

At the distoventral margin of the uropod protopodite near the bases of the uropod rami of *Metaphreatoicus, Colubotelson* and *Mesacanthotelson* two conspicuous spines with spinose tips are developed which presumably are used for sensitive purposes (figs. 26–27). Species of the phreatoicidean genus *Crenoicus* (WILSON & HO 1996) and *Onchotelson brevicaudatus* have one robust spinose seta at the ventrodistal margin of the uropod protopodite. Correspondingly located spines also are present in *Phreatoicopsis* (2 spines), *Mesamphisopus* (2 spines) and *Paramphisopus* (1 spine), however, the setae have simple tips and are not spinose at their ends. At the distal tip of the uropod protopodite in *Nichollsia kashiensis* no conspicuous spines are present but only two slender hairs are developed. In the oniscidean species investigated so far (cf. ERHARD 1995, 1996, 1997) homologous spines are missing. Presumably, the different character states present in the Phreatoicidea have to be considered as features of subordinate groups (cf. WILSON & KEABLE in press).

– Composition of the uropodal rami

The Oniscidea as well as most other isopods have uniarticulate uropodal rami which terminally may bear slender sensitive spines (cf. ERHARD 1995, 1996, 1997). Also, the uropodal rami of *Paramphisopus palustris, Mesamphisopus capensis* and adult specimens of *Nichollsia kashiensis* show only one article respectively which, in case of *Paramphisopus* and *Mesamphisopus,* are tightly packed with strong lateral and terminal spines. In contrast, the distal ends of the uropodal rami in *Metaphreatoicus* (fig. 26), *Colubotelson, Onchotelson, Mesacanthotelson, Phreatoicop-*

sis and newly hatched young specimens of *Nichollsia kashiensis* (cf. GUPTA 1989: 34, fig. 8) have separate tips. Those of *Onchotelson, Colubotelson, Phreatoicopsis* and young *Nichollsia* are strongly sclerotized spines which look like the claws of the pereiopod dactylopodites.
Corresponding structures are interpreted by NICHOLLS (1943: 22) as possible rudiments of retained distal articles. In the asellotan genus *Stenetrium* uropodal rami occur in which more than one joint is indicated (SEROV & WILSON 1995: 73). In representatives of the peracaridan outgroups "Mysidacea", Amphipoda, Spelaeogriphacea, Cumacea, Mictacea, Tanaidacea, (cf. SCHRAM 1986, GRUNER 1993) uropodal rami occur which are composed of two or more articles. On account of this pattern of characters it possibly might be that the plesiomorphous state within the isopodan groundpattern includes uropodal rami with vestigial distal articles.

– Relative length of the uropodal rami
In the oniscidean groundpattern the uropodal rami are about equal in size (ERHARD 1995: 95). This is also the case in *Metaphreatoicus* (fig. 26), *Colubotelson, Onchotelson, Mesacanthotelson* and newly hatched young specimens of *Nichollsia kashiensis,* however, the exopodite is always a little smaller than the endopodite (cf. GUPTA 1989: 34, fig. 8). In species of *Crenoicus* (WILSON & HO 1996), *Paramphisopus, Phreatoicopsis* and *Mesamphisopus* the uropod exopodites are clearly shorter than the endopodites (cf. NICHOLLS 1943: fig. 14, 27). In male adult specimens of *Nichollsia kashiensis* the uropod exopodite is about four times longer than the endopodite, in females they reach only the double length. The endopodite of the adult specimens are formed like inward curved claws. This feature is interpreted by GUPTA (1989: 44) as part of a defensive organ and might be a derived character state in respect to the phreatoicidean groundpattern.

– Composition of the uropod protopodite locomotors Mm 97 and 99
The fan-shaped uropod protopodite locomotors Mm 97 and 99 in the phreatoicids are strongly developed and consist of about 6–7 (*Metaphreatoicus, Onchotelson, Paramphisopus, Mesamphisopus*), 5–12 (*Phreatoicopsis*) or more than 12 bundles (*Nichollsia*). In contrast, the homologous muscles of the oniscidean species investigated so far by the author are composed of maximum 3 branches (figs. 24–25, 28–29; cf. ERHARD 1995, 1996, 1997). The powerful condition of the phreatoicidean muscles might be explained by their function as part of the motor for the pleotelsonic thrusts onto the substrate performed by phreatoicidean species. This behaviour was reported by GUPTA (1989: 12) on *Nichollsia* and by NICHOLLS (1943: 57) on *Hyperoedesipus*: "... the uropods may drag and kick upon the surface".

– Arrangement of the uropodal locomotors Mm 101–103
Within the uropod protopodites of *Metaphreatoicus, Onchotelson, Paramphisopus, Phreatoicopsis* and *Mesamphisopus* the uropod exopodite depressor M 101 is situated laterally to the muscles M 102 and M 103 (in *Nichollsia kashiensis* an exact determination of the muscle arrangement failed). In the Oniscidea M 101 always runs between the muscles M 102 and M 103 (figs. 28–29; cf. ERHARD 1995, 1996, 1997).

6. Phylogenetic-systematic position of *Nichollsia*

According to the literature data on the systematic position of the family Nicholl-siidae (e.g. Tiwari 1955, Knott 1986, Wägele 1989, Wilson & Keable, in press) the inclusion of the family in the suborder Phreatoicidea is widely accepted. However, most of the presumptive autapomorphous characters of the taxon Phreatoicidea (cf. Wägele 1989, Brusca & Wilson 1991, Erhard 1998a) are only present in non-nichollsiid phreatoicideans. These characters are the presence of long pleonal epimera, lateroventral pleotelsonic extensions, laterally flattened uropod protopodites and an upturned pleotelsonic apex forming together the ventral pleopodal chamber (cf. chapt. 5.2 and Erhard 1998a: 7) which is present in all surface-living and some hypogean phreatoicid species[2]). Furthermore, following Wilson & Keable (in press) *Nichollsia* lacks also the bifurcate spines in the mandibular spine row which, presumably, are found in all other phreatoicideans.

The lack of a phreatoicidean-like pleopodal chamber, presumably, represents an isopodan groundpattern character because it is restricted in its typical appearance only to the Phreatoicidea and does not occur in further in- and outgroups of the Isopoda. Therefore, it is questionable whether the lack of the pleopodal chamber in specimens of *Nichollsia* but also in species of the phreatoicidean genera *Hyperoedesipus, Phreatoicoides* and *Hypsimetipus* represents a primary feature or a secondary loss.

According to Knott (1986), Wägele (1990), Erhard (1998a: 7) and Wilson & Keable (in press) the above mentioned ground water forms and burrowers might be derived from surface-living phreatoicids and a reduction of the pleopodal chamber, presumably, represents an adaptation to the life in interstitial habitats. This hypothesis might be supported by the observation that lateroventral pleotelsonic extensions still are intimated in *Hyperoedesipus, Phreatoicoides longicollis, P. wadhami* (cf. Nicholls 1943: fig. 12, 31–32), *Hyperoedesipus* (Sayce 1902: pl. 18, fig. C) and newly hatched young specimens of *Nichollsia* (cf. Gupta 1989: 34, fig. 8).

Furthermore, phreatoicidean species actively use the strongly posteroventrally reflexed pleotelson in locomotion (e.g. *Crenoicus, Metaphreatoicus, Colubotelson, Paramphisopus)* performing amphipod-like pleotelsonic thrusts onto the substrate (cf. Erhard 1998a: 13). Equivalent pleotelsonic movements have been observed also in subterranean and burrowing phreatoicids as reported by Nicholls (1943) on *Hyperoedesipus plumosus* and by Gupta (1989:12) on *Nichollsia kashiensis.* As already discussed by Erhard (1998a: 40) this unique type of locomotion and the correlated extraordinary muscular and skeletal development of the vaulted and elongate pleotelson, presumably, has to be considered an apomorphous character complex of the Phreatoicidea (cf. Wilson & Ponder 1992: 294, Wilson & Keable, in press).

At the present state of knowledge, the described pattern of characters plead more for the close relationship of *Nichollsia, Hyperoedesipus, Phreatoicoides* and *Hypsimetopus* with all other phreatoicidean species and for the monophyly of the taxon

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[2]) The scoring of the character "styliform uropods" as an autapomorphous status of the Phreatoicidea (Wägele 1989) was criticized recently (Wilson 1996) and, probably, has to be reassessed. As discussed already in Erhard (1998a: 9), the character "enlargement of the pleon segment V" (cf. Brusca & Wilson 1991) appears to be a weak argument to substantiate the monophyly of the Phreatoicidea s. str. because this character also occurs within the isopodan taxa *Tainisopus* and Anthuridea.

Phreatoicidea than for an isolated systematic position of these hypogean forms. For the time being, the lack of a pleopodal chamber and the "phreatoicidean-typical" appearance in *Nichollsia,* therefore, is interpreted as a derived feature evolved during the invasion of hypogean habitats by ancestors of *Nichollsia,* and not as a primitive character state.

In this connection, an interesting observation on the Indian species *Nichollsia kashiensis* and the South African *Mesamphisopus capensis* is worth mentioning. Both species share some identical conditions of anatomical characters which are not present in the other phreatoicidean species investigated within the present research program (cf. chapt. 2.1.).

These character states are: (**1**) The complete lack of the medioventral sternal processus at the pereion and pleon segments (ERHARD 1998a: 10), (**2**) the identical pattern of the bundles in the tergosternal parts of the muscles Mm 3, 7, 105–108 within the central layer of the ventral longitudinal musculature (ERHARD 1998a: 24), (**3**) the identical composition of the pleopod remotors Mm 2, 6, 9, 11 and 13 which are formed by 4 bundles respectively (ERHARD 1998a: 33), (**4**) the "distally shifted" position of the appendix masculina at the proximal pleopod endopodite II-article (chapt. 4.2.2.) and (**5**) the complete lack of the anterior apophyses of the pleopod protopodites. However, the latter character state also could be shown in *Paramphisopus palustris* (ERHARD 1998a: 12).

The polarity assessment might describe the characters 1 and 5 in all probability as apomorphies (ERHARD 1998a: 10, 12) but on account of their reductive nature a convergent development in *Nichollsia* and *Mesamphisopus* cannot be excluded. Remarkable are the characters 3 and 4 because in the other investigated phreatoicids numerous different conditions of muscle compositions could be shown. However, clear statements on the character polarity are difficult to assess at the present state of knowledge on account of the limited selection of investigated species.

Nevertheless, the above mentioned characters, probably, may stimulate the consideration on the possibility of a close phylogenetic relationship of *Nichollsia* and *Mesamphisopus.* This idea would correspond with the commonly accepted hypothesis that, during the breakup of Gondwana, Africa, Madagascar and India have had contact much longer with each other than with Australia. Presumptive synapomorphies of *Nichollsia* and *Mesamphisopus,* not present in phreatoicids of the Australian region, then could have been evolved after the separation of Africa, India and Madagascar from Australia and Antarctica in common ancestors of both groups. These hypothetical ancestors, presumably, would have looked like *Mesamphisopus* with long pleonal epimera and the typical pleotelson and lateral flattened uropod protopodites. This would imply that the invasion into interstitial aquatic habitats and the development of a worm-like body shape by the ancestors of *Nichollsia* must have happened independently from equivalent developments for instance in stemlines of *Hyperoedesipus, Phreatoicoides* and *Hypsimetopus.*

It is specially emphasized, that the described scenario is not substantiated by well-founded characters. Another, probably more convincing hypothesis concerning the phylogeny of *Nichollsia* describes the close relationship to the ground water form *Hyperoedesipus* and the surface-burrowers *Hypsimetopus* and *Phreatoicoides* (cf. WILSON & KEABLE, in press). Presumptive synapomorphies of these taxa could be characters which evolved during the invasion of hypogean habitats like the lack of

eyes or the worm-like appearance. Obviously, the phreatoicidean pleopodal chamber formed by long pleonal epimera and lateroventral extensions of the pleotelson as well as lateral pleopod epipodites and a projected pleotelsonic apex as functional units of the character complex "pleopodal chamber" lose their importance and were reduced in interstitial habitats. However, these characters are of reductive nature and the possibility of a convergent evolution caused by an independent change of habitat cannot be weakened. Therefore, future investigations are necessary to look for well-founded positive characters to clarify the inconsistencies in reconstructing the phylogeny of *Nichollsia.*

7. Conclusions

7.1. Groundpattern characters

7.1.1. Male pleopod endopodite II

The male pleopod endopodite II in the isopodan groundpattern is devided into a mediodistal appendix masculina and a proximal leaf-like joint. The distal part of the leaf-like article is retained in the Phreatoicidea what might represent a plesiomorphous groundpattern character of the group. In contrast, the complete reduction of this distal part in the Oniscidea has to be considered as an apomorphous condition (chapt. 4.2.2.).

In the oniscidean and phreatoicidean groundpatterns a dicondylic articulation is present between the proximal endopodite II-article and the appendix masculina (chapt. 4.2.2.).

In the phreatoicidean and oniscidean groundpatterns the anterior wall of the appendix masculina is deepened and is forming a channel for the distally directed transport of spermatophores. In the highly modified appendix masculina of *Nichollsia* a corresponding channel is missing (chapt. 4.2.2.).

Within the oniscidean groundpattern the appendices masculinae have linear shapes whereas the distal parts of the phreatoicidean gonopods are curved laterally. A cooperation of both appendices masculinae during copulation, presumably, represents an oniscidean groundpattern character which is not confirmed for the Phreatoicidea (chapt. 4.2.2.).

In the Phreatoicidea only one locomotor of the male pleopod endopodite II, M 61, is present whereas in the oniscidean groundpattern two locomotors, Mm 60 and 61, are developed. The latter condition, presumably, might represent an apomorphy of the Oniscidea in respect to the isopodan groundpattern (chapt. 4.2.2.).

The presence of the muscle M 62 serving as locomotor of the appendix masculina is assumed to be a groundpattern character of the Phreatoicidea and the Oniscidea (chapt. 4.2.2.).

7.1.2. Skeleton of the pleopods I–V

The occurrence of two pleopod protopodite joints in the Phreatoicidea is interpreted as a plesiomorphous condition of the group. In contrast, the presence of only one protopodite article in the Oniscidea presumably represents an apomorphy in respect to the isopodan groundpattern (chapt. 4.4.1.).

The existence of dicondylic articulations between the pleopod protopodites and endopodites I–V and the presence of sclerotized basal endopodite regions is assumed to be a plesiomorphous condition in respect to the isopodan groundpattern. This character is retained in the phreatoicidean groundpattern of all pleopods and in the male pleopods II of the Oniscidea. A reduction of articular points between protopodites and endopodites and the lack of sclerotized basal endopodite regions then has to be interpreted as an apomorphous character state which is present at least in the oniscidean pleopods III–V (chapt. 4.4.1.).

Between the protopodites and the exopodites dicondylic articulations are assumed to occur in the groundpatterns of the phreatoicidean pleopods I–V and the onoscidean pleopods III–V. In contrast, the existence of monocondylic articulations in the oniscidean pleopods I and II, presumably, represents an apomorphous feature (chapt. 4.4.1.).

The presence of posterior lobes of the pleopod protopodites III–V for guiding the pleopod exopodites III–V, presumably, represents an apomorphous character state of the Oniscidea in respect to the Phreatoicidea (chapt. 4.4.1.).

Within the isopodan and phreatoicidean groundpatterns the pleopod exopodites II–V are composed of two articles. The distal joint is still movable. In the Phreatoicidea the articulation between both segments is narrow which might be an autapomorphous character state of the group (cf. Wilson & Ponder 1992: 295). In the Oniscidea all exopodites consist of one article which might represent an apomorphous condition in respect to the isopodan groundpattern (chapt. 4.4.1.).

In the phreatoicidean groundpattern the basal exopodite regions of the pleopods II–V (probably I–V) have medial and lateral lobes. In the Oniscidea a comparable character could not be found (chapt. 4.4.1.).

The presence of lateral epipodites at all five pleopod protopodites represents a groundpattern character of the Isopoda. In the phreatoicidean groundpattern epipodites occur at the pleopods II–V and, presumbably, at the pleopod I. In the oniscidean groundpattern the lateral epipodites of the pleopods III–V are largely reduced which has to be considered as an apomorphy (chapt. 4.4.1.).

The presence of coupling setae on medial lobes of the distal pleopod protopodite articles I–V might be a groundpattern character of the Phreatoicidea. Corresponding structures are missing in the Oniscidea which might be an apomorphous character (chapt. 4.4.1.).

7.1.3. Musculature of the pleopods I–V

In the Phreatoicidea, the intrinsic pleopod promotors (M 48, Mm 58/59, Mm 71/72 within the pleopods I–III) are stretched between the proximal and distal pleopod protopodite articles (equivalent conditions could be shown for the pleopods IV–V). In the Oniscidea the homologous muscles run between the sternites and the pleopod protopodites which represents an apomorphous status in respect to the phreatoicidean condition (chapt. 4.4.2.).

The presence of interarticular protopodite muscles (Mm 115, 119–120, 124–125 within the pleopods I–III) represents a plesiomorphous groundpattern character of the Phreatoicidea whereas the lack of corresponding muscles in the Oniscidea might be explained by secondary reduction (chapt. 4.4.2.). An equivalent situation has to be assumed for the interarticular protopodite muscles Mm 116 (pleop. I), 122 (pleop. II) and 123 (pleop. III) (chapt. 4.4.2.).

The complete reduction of the medial locomotor of the pleopod exopodite II, M 118, might represent an apomorphous character state of the Oniscidea. The Phreatoicidea seem to be apomorphous concerning the complete reduction of the medial exopodite locomotor M 76 inside the pleopods III. Concerning the composition of the medial exopodite locomotor within the pleopods III, M 79, the Phreatoicidea have retained the plesiomorphous character state with two bundles originating on the proximal and distal protopodite articles. The Oniscidea might show the apomorphous status with only one branch which might be caused by the fusion of the protopodite articles (chapt. 4.4.2.).

The lateral exopodite locomotors in the pleopods II–V (Mm 65/66, 77/78, 87/88, 95/96) in the phreatoicids have their origin posteriorly on the proximal as well as on the distal protopodite article. Within the Oniscidea the protopodites are no more biarticulated wherefore a phreatoicidean-like differentiation of the muscle origins does not occur. This feature has to be considered as an apomorphous status (chapt. 4.4.2.).

The pleopods I–III of the Phreatoicidea have one intrinsic endopodite muscle respectively (M 117, M 121, M 126). Within the Oniscidea homologous muscles could not be shown (chapt. 4.4.2.).

7.1.4. Skeleton of the uropods

The insertion of the uropods at the anteriorly positioned ventrolateral pleotelsonic extensions in the Phreatoicidea is assumed to be a plesiomorphous character state in respect to the isopodan groundpattern. The subterminal insertion present in the Oniscidea, presumably, might be an apomorphous condition (chapt. 5.2.).

The formation of a ventral pleopodal chamber by downward developed pleon epimera, anterior lateroventral pleotelsonic extensions, laterally flattened uropod protopodites, the dorsally curved pleotelsonic apex as well as the adjacent regions of the caudal pleotelsonic margin has to be considered an apomorphous groundpattern character of the Phreatoicidea. Originally, it might have a protective action against pollution of the respiratory pleopods by muddy water and might favour the supply of the pleopods with oxygen (chapt. 5. 2.).

Within the oniscidean groundpattern the uropod protopodites are movable in lateral and medial direction on account of a dorsoventral articular axis. The apophyses of the protopodite locomotors are situated laterally and medially to the articular axis. The uropod protopodites within the phreatoicidean groundpattern are movable in dorsomedial and ventrolateral directions. The points of articulation between pleotelson and uropod protopodite are forming an axis which passes from ventromedial to lateral and the protopodite apophyses are situated ventrolaterally and dorsomedially (chapt. 5.2.).

Styliform uropods are developed in the isopodan taxa Phreatoicidea, Oniscidea, Asellota (incl. Microcerberidae), Bopyridae and *Tainisopus* whereas in the "Flabellifera", Gnathiidae and Anthuridea broad and flat uropods are present which are forming a tail fan (chapt. 5.2.).

As an apomorphous groundpattern character of the Phreatoicidea the uropod protopodites are flattened laterally and contribute to the formation of the pleopodal chamber (chapt. 5.2.). In the oniscidean groundpattern the protopodites are flattened in the dorsoventral plane or show a sub-circular sectional view.

In the Phreatoicidea the dorsal walls of the uropod protopodites have medial and lateral longitudinal ridges. In the Oniscidea comparable ridges are missing (chapt. 5.2.).

The distal ends of the uropodal rami in the phreatoicidean groundpattern, possibly, have separate tips which might represent vestigial distal articles (chapt. 5.2.).

7.1.5. Musculature of the uropods

In the Oniscidea the locomotors of the uropod protopodites Mm 97–100 take their origin at the pleotelsonic tergite and sternite. In contrast, the homologous muscles of the Phreatoicidea are attached at the side-walls of the anterior lateroventral pleotelsonic extensions which might be an autapomorphy of the group (chapt. 5.2.).

Within the phreatoicidean groundpattern the uropod locomotors M 97 and M 99 are strongly developed and consist at least of 6 bundles. The powerful condition of the muscles might be explained by their function as part of the motor for the pleotelsonic thrusts. The homologous muscles of the Oniscidea are composed of maximum 3 branches (chapt. 5.2.).

Within the phreatoicidean groundpattern the uropod exopodite depressor M 101 is situated laterally to Mm 102–103. In the Oniscidea M 101 always runs between the muscles M 102 and M 103 (chapt. 5.2.).

7.2. Apomorphies

7.2.1. Phreatoicidea

The following autapomorphies of the Phreatoicidea could be found which might substantiate the monophyly of the group: The narrow articulation between the exopodite joints of the pleopods II–V (chapt. 4.4.1.; Wilson & Ponder 1992: 295), the formation of a ventral pleopodal chamber by downward developed pleon epimera, anterior lateroventral pleotelsonic extensions, laterally flattened uropod protopodites, the dorsally curved pleotelsonic apex as well as the adjacent regions of the caudal pleotelsonic margin (chapt. 5.2.) and the origin of the uropod protopodite locomotors Mm 97–100 at the side-walls of the anterior lateroventral pleotelsonic extensions (chapt. 5.2.).

The presence of another presumptive apomorphous character of the Phreatoicidea in further isopod groups has to be tested by future anatomical studies. This character concerns the lack of the pleopod exopodite III locomotor M 76 (chapt. 4.4.2.).

7.2.2. Oniscidea

The presence of the following apomorphies of the Oniscidea in other isopod taxa still has to be checked by further ingroup comparisons: The complete reduction of the distal leaf-like part of the proximal pleopod endopodite II-article in male specimens (chapt. 4.2.2.), presumably, the complete linear shape of the appendix masculina and the functional cooperation of the gonopods of both sides (chapt. 4.2.2.), the presence of two locomotors Mm 60 and 61 of the male pleopod endopodite II (chapt. 4.2.2.), the presence of only one protopodite article in the pleopods I–V (chapt. 4.4.1.), the reduction of the articular points between protopodites and endopodites and the lack of sclerotized basal endopodite regions within the pleopods I–V (chapt. 4.4.1.), the existence of monocondylic articulations between the protopodites

and exopodites of the pleopods I and II (chapt. 4.4.1.), the presence of posterior lobes of the pleopod protopodites III–V for guiding the pleopod exopodites III–V (chapt. 4.4.1.), the lack of distal joints in the pleopod exopodites II–V (chapt. 4.4.1.), the lack of pleopod epipodites at the pleopods III–V (chapt. 4.4.1.), the lack of medial lobes with hooked setae at the pleopod protopodites (chapt. 4.4.1.), the pass of the pleopod promotors M 48, Mm 58/59, Mm 71/72 (pleopods I–III) which are stretched between the sternites and the protopodites (chapt. 4.4.2.), the lack of the interarticular protopodite muscles Mm 51/115, 64/119–120, 75/124–125 within the pleopods I–III (chapt. 4.4.2.), the lack of the pleopod exopodite II locomotor M 118 (chapt. 4.4.2.), the composition and point of origin of the pleopod exopodite III locomotor M 79 (chapt. 4.4.2.) and the subterminal position of the uropods at the pleotelson (chapt. 5.2.).

7.3. Characters of uncertain polarity

In case of several characters of the phreatoicidean and oniscidean pleonal limbs the polarity still has to be determined by in- and outgroup comparisons. These concern the presence of medioproximal and lateroproximal lobes at the pleopod exopodites II–V (probably I–V) in the Phreatoicidea and the lack of corresponding structures in the Oniscidea (chapt. 4.4.1.), the existence of the intrinsic endopodite muscles Mm 117, 121 and 126 within the pleopods I–III (chapt. 4.4.2.), the position of the points of articulation and the muscular apophyses at the insertion region of the uropod protopodites and the possible directions in movement of the uropods (chapt. 5.2.), the general shape of the uropods (chapt. 5.2.), the existence of dorsal longitudinal ridges of the uropod protopodites (chapt. 5.2.), the separation of the tips of the uropodal rami (chapt. 5.2.), the development and the composition of the uropod protopodite locomotors M 97 and M 99 (chapt. 5.2.) and the spatial arrangement of the locomotors of the uropodal rami Mm 101–103 (chapt. 5.2.).

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